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(*Recognosce notum, ignotum inspice*)

TRANSACTIONS

Edited by

J. RAMSBOTTOM, B. BARNES and H. WORMALD

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VOLUME XXIV JUNE 1940 PART I

THE ARUNDEL FORAY

19–20 May 1939

BY C. G. C. CHESTERS

THE President, Mr E. W. Mason, and a small party of members gathered at the Norfolk Hotel on Friday evening, 19 May 1939, for the spring foray. The weather was dry and warm and did not inspire those present with the hope of extensive collections of fungi during the week-end.

On Saturday and Sunday the lower and upper reaches, respectively, of Rewell Wood were visited. The fungi collected during Saturday were mainly common species. *Geaster fimbriatus* was found under some conifers on the west ridge of the wood. On Sunday certain interesting finds were recorded. After some search *Nummularia lutea*, on box, was discovered in quantity near the site at which it had been collected previously but *Rosellinia Buxi* which was then found with it on that host was not observed on this foray. In the beeches on top of the west ridge *Hypoxylon cohaerens* was plentiful on some of the lying timber and *H. rubiginosum*, more characteristic of ash, was quite abundant on fallen beech branches. *Nummularia Bulliardi* was a worthwhile find on some smaller branches of beech on the west side of this ridge.

Paine's Wood was visited on Monday and provided many of the recorded resupinates but was rather dry to yield a crop of microfungi.

At a meeting of members held after tea on Sunday it was decided that the spring foray in 1940 should be held, if possible, in the Marlborough district. The President proposed that a hearty vote of thanks be accorded to His Grace the Duke of Norfolk for permission to visit and collect in Rewell Wood and Paine's Wood. This was carried with acclamation.

Because of the adverse weather conditions the list of species is very short, and I am indebted to Mr Mason, Mr Pearson, Dr Smith and other members present for their records on which this list is based.

*List of species gathered during the Foray**

A. = Arundel; *P.* = Paine's Wood; *R.* = Rewell Wood.

HYMENOMYCETES

Armillaria mellea (Vahl) Fr. (rhizomorphs), *P.*, *R.*, mucida (Schrad.) Fr., *A.*
Auricularia auricula-Judae (Linn.) Schroet., *A.*, *R.*, mesenterica (Dicks.) Fr., *A.*, *R.*
Bourdotia Eyrei Wakef., *A.*
Coprinus micaceus (Bull.) Fr., *A.*, *R.*
Corticium Sambuci (Pers.) Fr., *A.*, tulasnelloideum v. H. & L., *A.*
Cortinarius (Hydrocybe) castaneus (Bull.) Fr., *A.*
Dacromyces deliquescens (Bull.) Duby, *A.*, *R.*
Daedalea quercina (Linn.) Fr., *A.*, *P.*
Eichleriella spinulosa (Berk. & Curt.) Burt., *A.*
Exidia Thuretiana (Lév.) Fr., *A.*
Fomes annosus Fr., *A.*, *R.*, ferruginosus (Schrad.) Mass., *A.*
Galera tenera (Schaeff.) Fr., *A.*
Gleocystidium porosum Berk. & Curt., *A.*, praetermissum (Karst.) Bres., *A.*
Grandinia farinacea (Pers.) Bourd. & Galz., *A.*
Hymenochaete rubiginosum (Dicks.) Lév., *A.*, tabacina (Sow.) Lév., *P.*
Hypholoma fasciculare (Huds.) Fr., *A.*, *P.*, sublateritium (Schaeff.) Fr., *P.*
Irpex obliquus (Schrad.) Fr., *A.*
Lenzites betulina (Linn.) Fr., *A.*
Marasmius funicularis (Fr.) Rea, *A.*, dryophilus (Bull.) Karst., *A.*, *P.*, *R.*
Merulius rufus (Pers.) Fr., *A.*
Naucoria semi-orbicularis (Bull.) Fr., *A.*
Odontia papillosa (Fr.) Bres., *A.*
Panus stipticus (Bull.) Fr., *A.*
Peniophora cinerea (Fr.) Cke., *A.*, crema Bres., *A.*, glebulosa Bres., *A.*, hydnoides Cke. & Mass., *A.*, laevigata (Fr.) Mass., *A.*, longispora (Pat.) Fr., *A.*, setigera (Fr.) Bres., *A.*, velutina (DC.) Fr., *A.*
Pholiota marginata (Batsch) Fr., *A.*, togularis (Bull.) Fr. *A.*
Pleurotus sapidus Schulz. *A.*, *R.*
Polyporus adustus (Wild.) Fr., *A.*, betulinus (Bull.) Fr., *R.*, caesius (Schrad.) Quél., *A.*, squamosus (Huds.) Fr., *A.*, *R.*
Polystictus versicolor (Linn.) Fr., *A.*, *P.*
Poria farinella Fr., *A.*
Psathyra fatua Fr., *A.*, obtusata Fr., *A.*
Solenia anomala (Pers.) Fr., *P.*, candida (Hoffm.) Fr., *A.*
Stereum hirsutum (Willd.) Fr., *A.*, *P.*
Trametes mollis (Sommerf.) Fr., *P.*, *R.*
Tremella mesenterica (Retz.) Fr., *P.*
Tricholoma gambosum Fr., *A.*

GASTEROMYCETES

Geaster fimbriatus Fr., *R.*

UREDINALES

Kuehneola albida Magnus, *R.*
Melampsora Euonymi-caprearum Kleb., *R.*
Puccinia Buxi DC., *R.*, obtegens (Link) Tul., *A.*, Violae (Schum.) DC., *R.*

* In some instances, where no precise location for a species had been given, it is listed under Arundel, thus covering both Rewell Wood and Paine's Wood.

USTILAGINALES

Urocystis Anemones (Pers.) Schroet., *P.*

PYRENOMYCETES

Anthostoma gastrinum (Fr.) Sacc., on *Ulmus*, *R.*
Cryptosphaeria eunomia (Fr.) Fuck., *R.*
Daldinia concentrica (Bolt.) Ces. & de Not., *R.*
Diatrype disciformis (Hoffm.) Fr., *P.*, *R.*, Stigma (Hoffm.) Fr., on *Fagus*, *P.*, *R.*, on *Corylus*, *R.*
Diatrypella favacea (Fr.) Ces. & de Not., on *Betula*, *R.*, on *Corylus*, *R.*, on *Fagus*, *P.*, *R.*
Eutypa spinosa (Pers.) Tul., on *Fagus*, *R.*
Eutypella stellulata (Fr.) Sacc., on *Ulmus*, *R.*
Hypoxylon coccineum Bull., *P.*, *R.*, cohaerens (Pers.) Fr., *R.*, fuscum (Pers.) Fr., on *Corylus*, *P.*, *R.*, Howieanum Pk., on *Corylus* and *Aesculus*, *P.*, rubiginosum (Pers.) Fr., on *Fraxinus* and *Fagus*, *P.*, *R.*, semi-immersum Nits., *R.*, serpens (Pers.) Fr., on *Fraxinus* and *Aesculus*, *P.*, on *Fagus*, *R.*
Melanomma Pulvis-pyrius (Pers.) Fuck., on *Fraxinus*, *R.*
Nummularia Bulliardi Tul., on *Fagus*, *P.*, lutea (A. & S. ex Fr.) Nits., *R.*
Pseudovalsa lanciformis (Fr.) Ces. & de Not., *R.*
Quaterneria dissepta (Fr.) Tul., *R.*, quaternata (Pers.) Schroet., *P.*, *R.*
Strickeria obducens (Fr.) Wint., *R.*
Ustulina vulgaris Tul., on *Fagus*, *P.* (conidial), *R.*
Xylaria carpophila (Pers.) Fr., *R.*, Hypoxylon (Linn.) Grev., *P.*, *R.*

DISCOMYCETES

Chlorosplenium aeruginosum (Oeder.) de Not., *mycelium*, *P.*
Ciliaria scutellata (Linn.) Quél., *A.*, *R.*
Dasyscypha nivea (Hedw. fil.) Sacc., *A.*, virginea (Batsch) Fuck., on *Fagus*, *R.*
Hyalina inflatula (Karst.) Boud., *A.*
Molisia cinerea (Batsch) Karst., *P.*, *R.*
Orbilia leucostigma Fr., *R.*

DEUTEROMYCETES

Coniothecium betulinum Corda, *R.*
Torula antennata Pers., on *Fraxinus*, *P.*, *R.*
Tuberculina persicina (Ditm.) Sacc., *R.*

MYCETOZOA

Ceratiomyxa fructiculosa Macbr., *R.*
Lycogala epidendrum Fr., *R.*

PHYTOPATHOLOGICAL EXCURSION, 1939

By G. C. AINSWORTH

The sixteenth annual Phytopathological Excursion took the form of a visit to the Hawthorndale Laboratories at the Jealott's Hill Research Station on Saturday, 17 June. The kindness of Imperial Chemical Industries, Ltd., in making this visit possible, and their generosity in providing lunch and tea, were greatly appreciated by a party of about thirty members and friends.

The principal feature of the day was a series of demonstrations and exhibits of the methods by which new and improved fungicides are evolved. The first stage takes place in the laboratory where each year many hundreds of compounds are subjected to certain routine tests to ascertain their fungicidal value against several common parasitic and saprophytic fungi. A small number of the more promising compounds are given a more extensive laboratory study but few reach the stage of small scale greenhouse trials and even fewer the experimental field trials.

Different classes of fungicides, such as wood preservatives and cereal grain disinfectants, are elaborated in different sections of the laboratories, and studies are also made on the effects of spreaders and other constituents of commercial sprays and dusts on fungicidal values.

The visitors found many details of interest in the laboratory, greenhouses and field and spent an enjoyable day.

ANNUAL MEETING

16 December 1939

OWING to the outbreak of war and the consequent difficulties of road transport the Council decided that it was not advisable to hold the Annual General Meeting and Autumn Foray which had been arranged for 25–30 September at Chipping Campden. Also the remainder of the 1939 programme—three Saturday forays and the November London meeting—had to be abandoned.

The postponed Annual Meeting was held on 16 December 1939, in the rooms of the Linnean Society at Burlington House, Piccadilly, by kind permission of the President and Council.

Dr H. Wormald was elected President for 1940. The retiring President, Mr E. W. Mason, the immediate past President, Miss K. Sampson, and Mr W. C. Moore were elected Vice-Presidents. The other officers and the editors were re-elected. The three new members of Council elected were Miss E. M. Blackwell, Dr G. E. Deacon, and Dr P. H. Gregory. The names of the proposed members of the Phytopathological Committee were read out and agreed to.

The Treasurer's statement was adopted.

It was decided to carry out a programme for 1940 as near normal as possible, though it was considered inadvisable to hold a Spring Foray or the usual day Forays. Two meetings will be held in London in spring, and one in autumn; the Phytopathological Excursion will also be arranged.

In a discussion on the place for the Autumn Foray it was agreed that somewhere should be chosen with collecting grounds within walking distance. Symonds Yat, Painswick, Arundel and Windsor were put forward as suggestions to be considered by the officers.

Dr René Maire, the eminent French mycologist, was proposed as honorary member by Mr Carleton Rea and seconded by Mr A. A. Pearson. He was elected with enthusiasm and unanimity.

After lunch the President, Mr E. W. Mason, M.A., F.L.S., gave his address "On specimens, species and names", after which tea was served.

The meeting was very well attended and members made full use of the much appreciated opportunity for discussing mycological, personal and international affairs.

J. RAMSBOTTOM.

RECEIPTS AND PAYMENTS FOR THE YEAR ENDING 30 JUNE 1939

1938		£	s.	d.
1 July.	Balance brought forward	637	11	10
1939				
30 June.	Subscriptions to date	329	6	8
	Gifts to Printing Fund	4	8	0
	Sale of *Transactions*:			
	Current volumes	105	16	6
	Back volumes	36	3	5
	Sale of Reprints	27	1	0
	Profit from sale of C. Rea's *British Basidiomycetae*	7	7	11
	Deposit Interest	3	5	0
	War Loan Interest...	17	10	0
		£1168	10	4

1939		£	s.	d.
30 June.	Cambridge University Press, Cost of 450 vol. XXII *Transactions* and Reprints ...	497	2	7
	Postage, Stationery, etc.:			
	Treasurer	2	10	9
	Secretary...	4	6	5
	Sec. Pathological Committee	3	1	0
	Editors	2	2	8
	Purchase of Addressograph	4	6	0
	Sundry Printing	4	19	6
	Fees of Meetings	6	3	6
	Cheesman Fund Allowance	5	0	0
	Balance in hand and on deposit	638	17	11
		£1168	10	4

CAPITAL ACCOUNT—Robinson Bequest, £50; Cheesman Fund, £150; Printing Fund, £300 — invested in 3½% War Loan

A. A. PEARSON, *Hon. Treasurer*

Examined and found correct, F. G. GOULD, 25 July 1939

The following have kindly sent gifts to the Printing Fund:

	£	s.	d.
Mr F. J. Barrington		5	0
Mr W. H. Edwards		5	0
Mr G. C. Hughes...		5	0
Col. C. T. Green		2	6
Dame Helen Gwynne Vaughan ...		10	0
Miss G. Lister	1	0	0
	£2	7	6

	£	s.	d.
Brought forward...	2	7	6
Mrs A. Montague		5	6
Dr G. Morgan		10	0
Dr G. H. Pethybridge		10	0
Prof. M. C. Potter		10	0
Mr E. W. Swanton		5	0
	£4	8	0

Some subscriptions are still unpaid. Please remit to the Hon. Treasurer.

A CHYTRID ALLIED TO *PLEOLPIDIUM INFLATUM* BUTLER

By GRACE M. WATERHOUSE
Royal Holloway College

(With 8 Text-figures)

Among the species of the Chytridiaceous genus *Pleolpidium* discovered by Butler (1907) infecting *Pythium intermedium*, one was described which differed from the others in having biflagellate zoospores. The species was named *Pleolpidium inflatum* pending the discovery of the resting spores, though Butler remarked that the two flagella separated it widely from the other species of the genus. Since this first description there has been, so far as I can ascertain, no printed record of its recurrence, though Dr F. K. Sparrow has written to say that he once found it in Paris. The present appearance of a similar parasite in this country is therefore interesting.

The parasite enters the host by means of zoospores which pierce the hyphal wall. The protoplasm passes in, mingles with that of the host and is indistinguishable from it. The sporangium of the parasite forms within what presumably would have been a sporangium of the host. The parasitic sporangium completely fills the host sporangium, and its wall is intimately fused with that of the host. The parasite causes little change in the form of the host apart from occasional hyphal swellings and a difference in the shape of the sporangium.

The parasite appeared in January 1938 during an investigation of the water moulds of the Hogsmill River (a Surrey tributary of the Thames), on a mould growing on tomato and grape skins in three separate cultures kept in different places. The tomatoes and grapes had been used either as bait in the river or for reinoculation experiments in the laboratory. After the fruits had broken up, the skins were kept from November to the end of January in glass jars with frequent changes of tap water and examined at intervals to ascertain whether any other moulds had appeared. During the fortnight preceding the appearance of the parasite, there had been an abundance of a proliferating species of *Phytophthora* on the grape. When the parasitic sporangia were noticed, portions of infected skin were transferred to Quaker Oat agar plates, and a good growth of the parasitized fungus was obtained. The host when separated from the parasite was found to resemble *P. cryptogea*.

Description of the parasitized fungus

On the fruit skins the hyphae were finer (2·5μ diam.) and the sporangia smaller than in culture, and pyriform (30μ long). There was little hypertrophy of the host hyphae. On Quaker Oat agar the hyphae were much coarser (up to 8μ diam.) and often swollen below the sporangium (Fig. 2 B). The hyphae were non-septate except in the older parts. Parasitized sporangia were produced sparingly on Quaker Oat agar, but when the plate was flooded with water, very numerous sporangia developed (600–800 per sq. cm., Fig. 1). They varied very much in shape and size, being pyriform or oval in fresh cultures (Fig. 2 A), and oval or spherical in older cultures (Fig. 2 C) (variation 25–74 × 18–48μ, the usual size being about 38 × 32μ). The

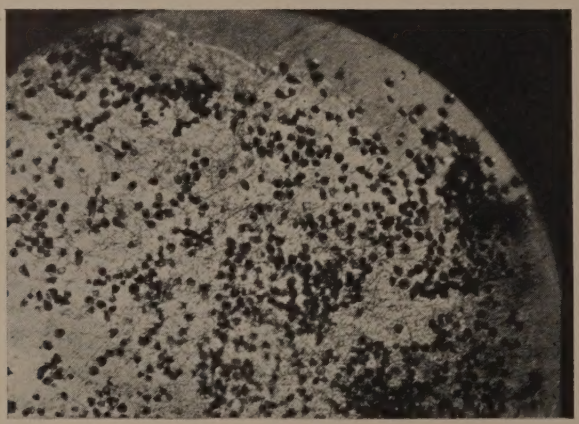

Fig. 1. Photomicrograph of a portion of an agar culture of the parasitized fungus showing the large numbers of sporangia produced after flooding with water, × 30.

sporangia were always terminal whether on the main hyphae or on short lateral branches. No intercalary ones were ever observed, and there was no sympodial growth or proliferation through empty sporangia. The wall of the sporangium was thick, about double the thickness of that of a normal sporangium of *Phytophthora*. Where the base of the sporangium passed into the supporting hypha there was sometimes a thick plug, 5μ deep (Fig. 2 A), or a hemispherical swelling protruding into the sporangium (Fig. 2 C), or occasionally two transverse walls (Fig. 3). The common wall turned pale purplish red with chlor-zinc-iodine. The inner wall of the sporangium of the parasite could not as a rule be distinguished from that of the host in any part, but in one isolated sporangium in a culture that had become

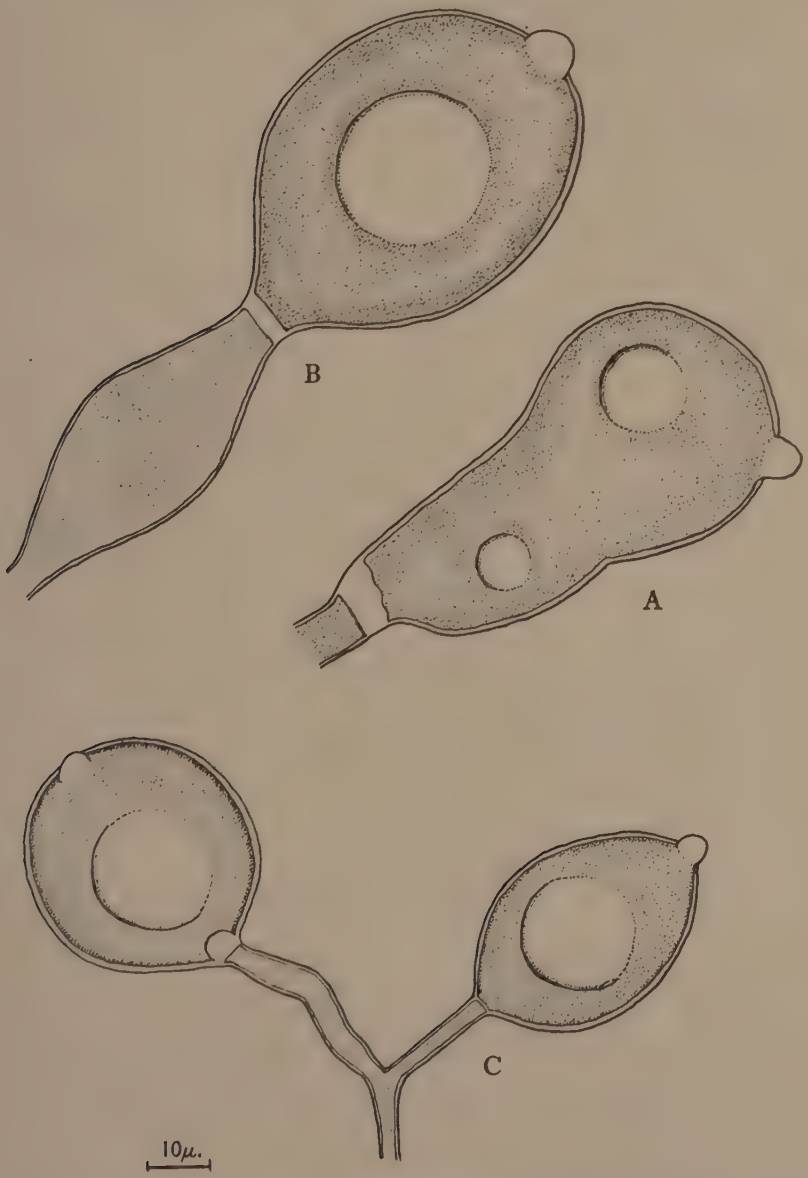

Fig. 2. Sporangia of the parasite. A. The usual shape in fresh cultures. B. With a swollen supporting hypha. C. Showing branching and a hemispherical basal plug.

partially dried, the entire parasitic sporangium with its papilla had contracted within the host sporangium, and it was outlined by a thin membrane (Fig. 4). The papilla was usually single though there were several examples with two (Fig. 3) and a few with three papillae. The papilla was usually terminal, or occasionally slightly lateral, and was hemispherical, arising so abruptly from the general contour of the

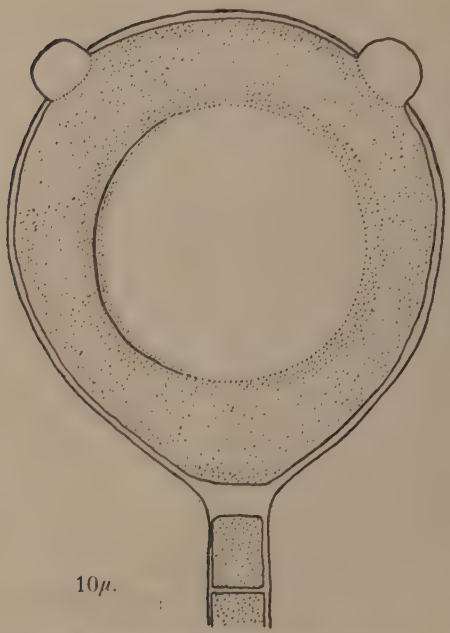

Fig. 3. Sporangium with two papillae and a double basal wall.

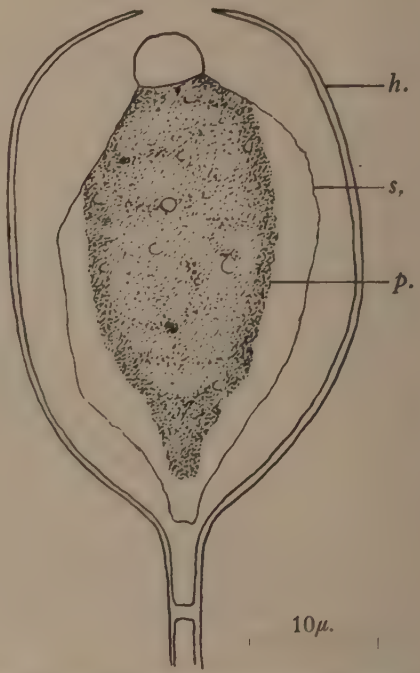

Fig. 4. Dried sporangium showing sporangium of parasite contracted within the host wall. *h*, host wall; *s*, wall of parasitic sporangium; *p*, protoplasm of parasite.

sporangium as to give the appearance of being stuck on. It stained deeply with cotton blue in lactic acid. The protoplasm of the hyphae and young sporangia was granular, and there was nothing to distinguish that of the parasite and host. Soon after the sporangium was delimited the protoplasm became pellucid with a large central vacuole (or occasionally several vacuoles) (Figs. 2, 3).

Development of sporangium of the parasite and emission of zoospores

The development of the parasitic sporangium at a hyphal tip and the emission of zoospores from several sporangia was observed in hanging-drop cultures (Fig. 5). The end of a hypha emerging from a portion of an agar culture began to swell about 4 p.m. By 10.30 the next morning the swelling was spherical and about four times the diameter of the hypha, and was cut off by a transverse wall. The protoplasm, which had been granular, now became clear and vacuoles appeared which changed in shape and moved about. The sporangium reached its full size by the evening, but the papilla did not appear at once and its growth was not observed. Fully developed sporangia mostly contained a large central vacuole. Upon the addition of fresh water the central vacuole dispersed, leaving the protoplasm quite clear except occasionally for a few small dark granules clustered near the centre (Fig. 6 B). Then the protoplasm was seen to be dividing up into what looked like zoospore initials but in ten minutes this appearance had vanished, the protoplasm again becoming clear. It remained so for about half an hour when the papilla vanished, so quickly that it was not observed whether it dissolved into the surrounding water or was drawn into the sporangium; the space which it had occupied in the wall could be seen quite clearly. Soon after this the protoplasm presented a finely reticulate appearance, and it was soon seen that the zoospores were being formed but the initials were much smaller (about a quarter of the size) than those seen earlier on (Figs. 6 D and 7 A, B). When the zoospores were quite clearly defined (in about half to three-quarters of an hour) a heaving movement began and the contents gradually moved round. This movement, very slow at first, gradually became faster until the zoospores were swirling rapidly round. The swarming continued for about ten minutes until suddenly the membrane across the pore left by the papilla burst, and out shot the zoospores at a remarkable speed, giving the effect of a miniature blizzard. The sporangium took some minutes to empty, and in spite of the large number (estimated at 1500–2000 in a medium-sized sporangium), it rarely happened that any zoospores were unable to escape.

It is probable that, owing to the adverse conditions in a hanging drop culture, the times given are somewhat longer than those that would elapse in a Petri dish or in nature.

Zoospores. The zoospores were 5–8μ long and pyriform, with two unequal flagella, the slightly longer one directed anteriorly and the other posteriorly (Fig. 7 D). The protoplasm was clear except for a few bright granules placed centrally or nearer the pointed end. The

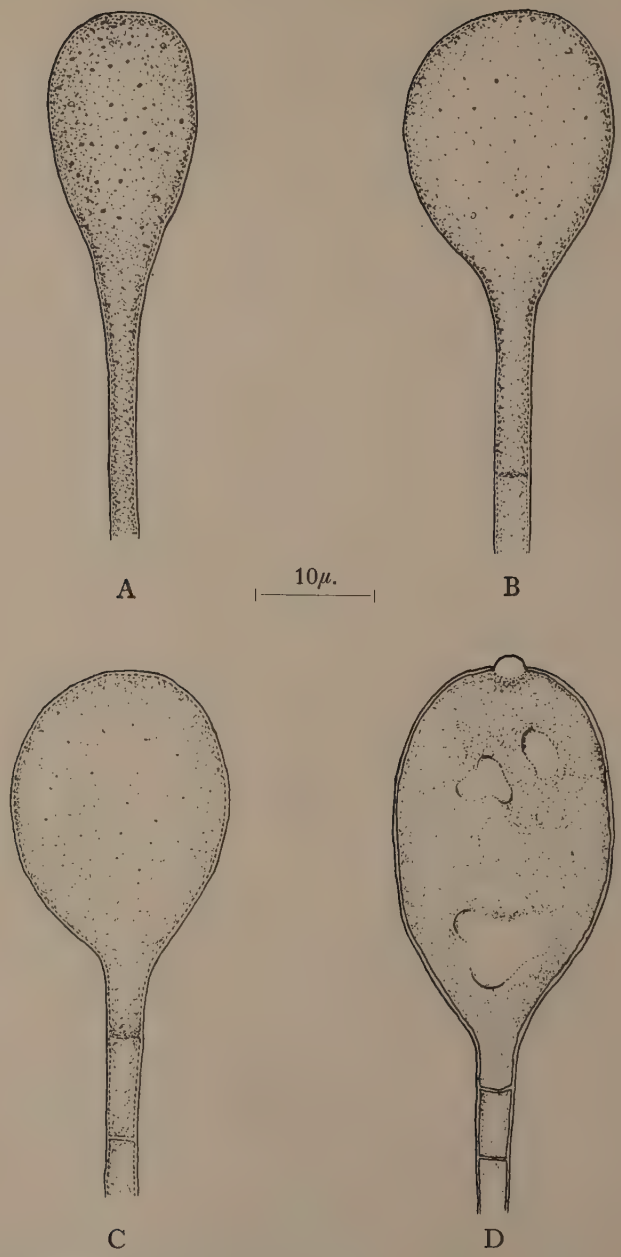

Fig. 5. Development of parasitic sporangium within the host. A. Swollen hyphal tip, 24 March, 4 p.m. B. Basal wall forming, 25 March, 10.30 a.m. C. Second basal wall forming, 25 March, noon. D. Fully formed sporangium with vacuoles continually changing in shape, 25 March, 7 p.m.

zoospores could swim for twenty-four hours or more if they did not reach suitable hyphae to infect. Many settled down in the water, rounded off and encysted. If, however, young hyphae were present the zoospores were soon seen hanging in rows on them. In be-

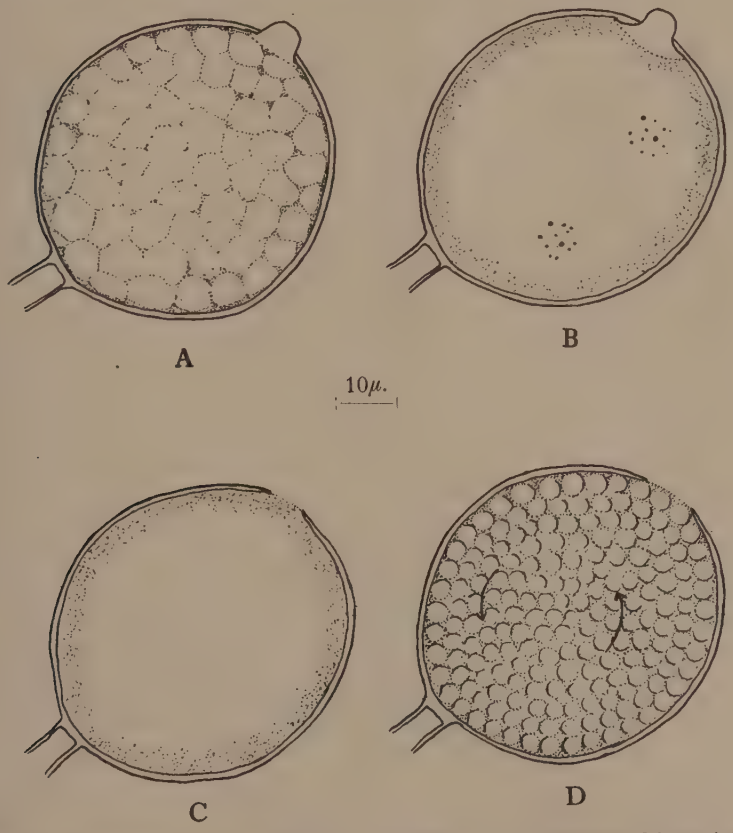

Fig. 6. Development of zoospores of the parasite. A. Appearance of large initials, 10.45 a.m. B. Resumption of clear appearance, 10.50–11.15 a.m. C. Disappearance of the papilla, 11.20–11.30 a.m. D. Zoospores swarming inside, 12.15–12.45 p.m.

coming attached to a hypha the zoospores seemed to hang on by means of the flagellum, the pointed end being directed to the hypha. Penetration was once observed. The zoospore after attaching itself gradually became flattened against the hyphal wall until it was hemispherical (Fig. 8). A slender tube was put out which pierced the wall and then the contents of the zoospore, now entirely granular,

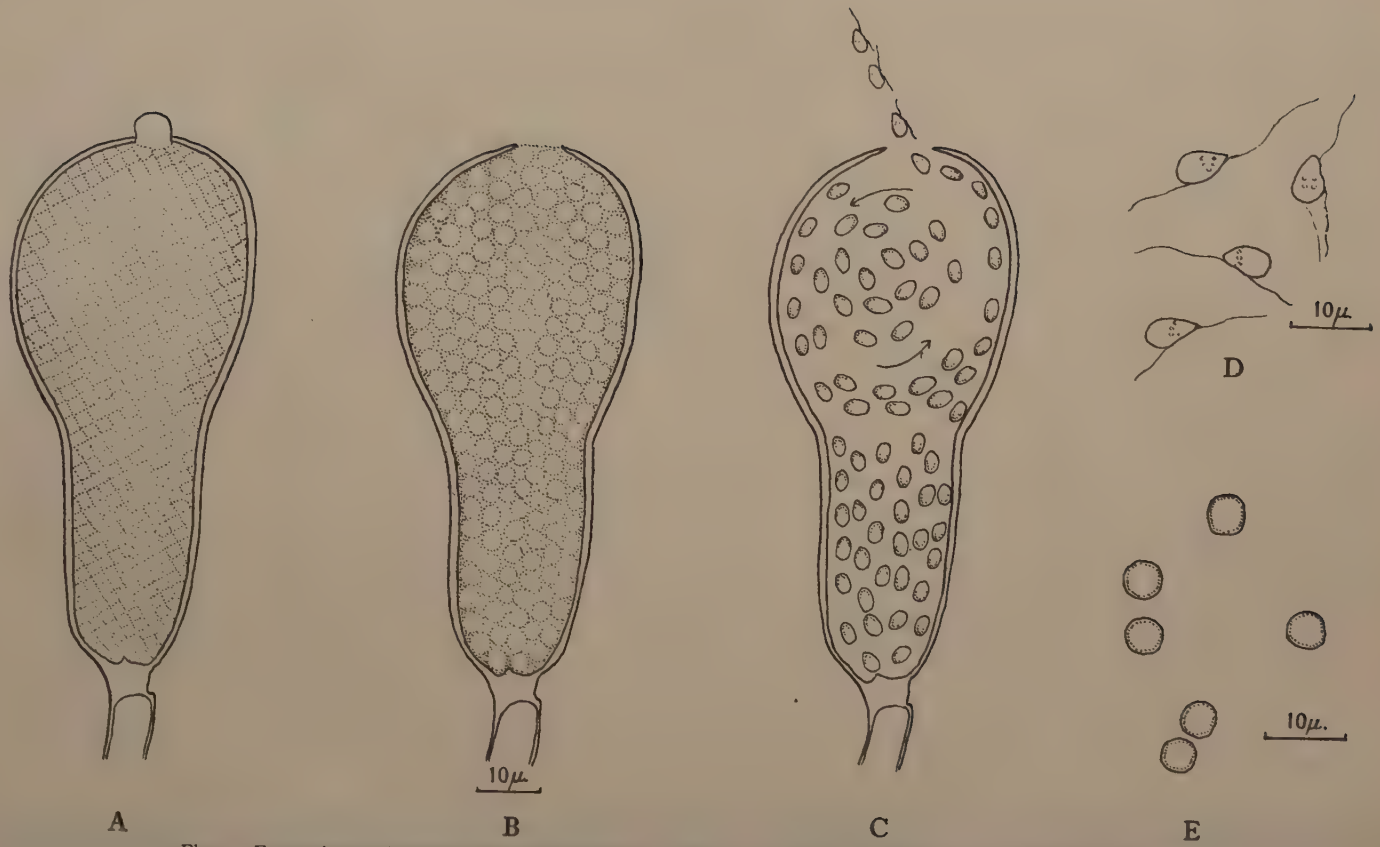

Fig. 7. Formation and release of zoospores of the parasite. A. Reticulate stage, 11 a.m. B. Zoospore initials. C. Release of zoospores, 1 p.m. D. Motile zoospores. E. Encysted zoospores.

passed gradually in, taking about twelve hours to do so in a hanging-drop culture. At first the penetrating protoplasm could be seen distinctly but soon it became indistinguishably intermingled with that of the host.

No resting spores were found either on fruit skins or in agar cultures even after two months.

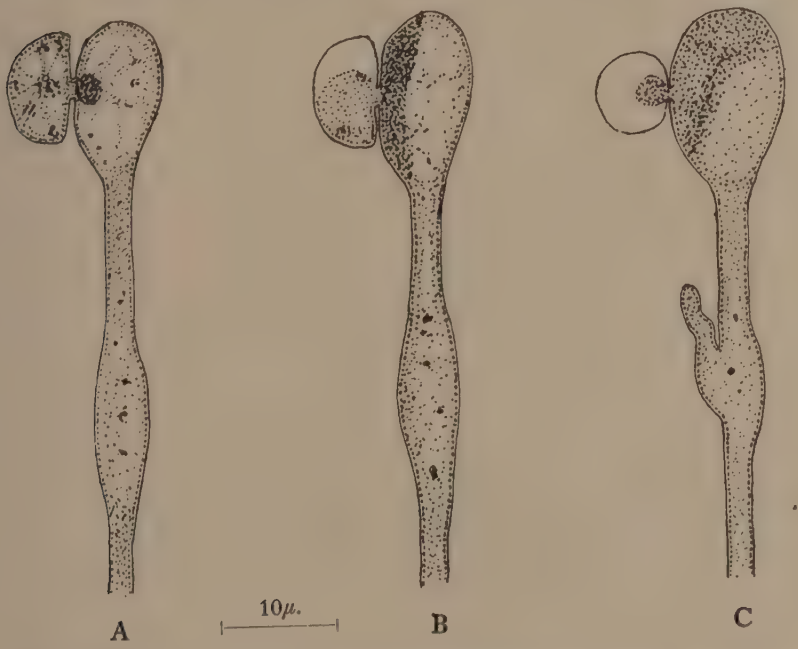

Fig. 8. Infection of a hyphal tip of the host by a zoospore of the parasite. A, 12.45 p.m.; B, 4.30 p.m.; C, 10.30 p.m.

Inoculation experiments

Altogether five inoculation experiments were successful. The hosts used were:

(*a*) The original host (probably *Phytophthora cryptogea*) obtained free from the parasite. This was achieved by taking portions from the edges of agar cultures of the parasitized fungus and transferring them to fresh plates of Quaker Oat agar. Some of these portions contained hyphae of the host not yet infected by the parasite and gave uninfected cultures of the host. These were used for reinoculation experiments with the parasite and three were successful.

(*b*) *Phytophthora megasperma*, obtained originally from a pond near Manchester. This was twice inoculated with the parasite.

Method. Portions were cut from the unparasitized agar culture, put in water and left for a day or two until a radiating hyphal growth had formed. One portion was then halved and to one half (called the host, *H*) was added either a portion of a parasitized agar culture or zoospores of the parasite only; the other half acted as a control (*C*). The water was changed at intervals. The first indication of activity of the parasite was the production or increased production by the host of normal sporangia emitting normal zoospores, the controls showing no such production or increase. The final proof was the production of parasitized sporangia in gradually increasing numbers on the radiating hyphae of the originally uninfected portion.

Details of inoculations of original host

Experiment 1.

3 March. Portions of uninfected mycelium put in water.
10 March. Radiating hyphal growth but no reproductive organs. Portions halved, zoospores of parasite put with one half (*H*), other half kept as control (*C*).
12 March. Normal sporangia on *H*, none on *C*.
15 March. Normal and parasitized sporangia on *H*: *C* with a few normal sporangia.
30 March. *H* covered with masses of sporangia of parasite.

Experiment 2.

20 March. 11 a.m. Portions of uninfected mycelium put in water, half (*H*) with parasitized mycelium, half as control (*C*).
20 March. 5 p.m. Numerous normal sporangia on *H*, none on *C*.
22 March. None as yet on *C*.
24 March. Parasitized sporangia on *H*: *C* with a few normal sporangia.

Experiment 3.

24 March. Portion of *C* from Exp. 2 put in water with zoospores of parasite.
1 April. Parasitized sporangia produced on this portion: rest of *C* with a few normal sporangia.

Details of inoculations of Phytophthora megasperma

Experiment 1.

18 March. Portion of uninfected mycelium (*H*) put in water with parasitized mycelium: similar portion left as control (*C*).
24 March. Parasitized sporangia very numerous on *H*: *C* had only sex organs.

Experiment 2.

15 March. Portion of uninfected mycelium put in water.
20 April. Radiating hyphae, no sporangia. Fresh water added and a portion of parasitized mycelium.
23 April. Parasitized sporangia on radiating hyphae. (No control.)

There were several inoculation experiments made on the original host and one on *P. megasperma* which induced no parasitism. This may

have been due to the reduced vigour of the parasite or of its zoospores, or to the reduced vigour of the hosts. Inoculations were tried on *Rhipidium continuum* on tomatoes, and on *R. americanum* on ash twigs and no parasitism was obtained. As the parasite disappeared during the following vacation it was not possible to test its pathogenicity for *Pythium intermedium*, the host on which Butler found the similar parasite. Therefore it was not possible to determine whether the present species was identical with *Pleolpidium inflatum*.

Conclusions

It is clear that the present parasite is not very specialized, as it has been shown to attack two species of Pythiaceous fungi. It is therefore possible that it might also parasitize species of *Pythium*, and be identical with *Pleolpidium inflatum*. The points of difference noticed in comparing it with Butler's description are:

(1) *Host.* Apart from the fact that it was found only on *Pythium intermedium*, Butler also noted that only soil-inhabiting species of *Pythium* were attacked and that an aquatic species of *Pythium* bearing a parasite was never seen. The present parasite has so far been found only on aquatic species of *Phytophthora*.

(2) *Hypertrophy.* The excessive hypertrophy of supporting hyphae described as due to *Pleolpidium inflatum* was not found in the present form: only a few supporting hyphae were slightly swollen.

(3) *Size of sporangium.* The diameter of the largest sporangium noticed by Butler was 85μ. The largest I found was 74μ. This difference is not so important because the size of the sporangium is very variable in both, and slightly different conditions such as higher temperature (Butler worked at Antibes) might make much difference in the activity of both host and parasite.

(4) *Zoospores.* The zoospores of the parasite of *Pythium* tended to be reniform: those in the present cultures were pyriform.

Discussion

There is no doubt that the parasite here described is either identical with or closely related to *Pleolpidium inflatum* Butler. The genus *Pleolpidium* was established by Fischer (1892) for certain species of Cornu's genus *Rozella* (1872). Sparrow (1938) suggested that in the renaming of the genus by Fischer, the name *Rozella* should have been kept for the species now called *Pleolpidium*, because these were more typical of the genus as Cornu diagnosed it. *P. inflatum*, however, cannot now be included in this genus because the zoospores are biflagellate. The flagellation of the zoospore is considered to be an important diagnostic feature, and as the other species of *Pleolpidium*

have uniflagellate zoospores, *P. inflatum* should be separated from them.

In modern systems of classification (Gaümann, 1925; Fitzpatrick, 1930) all the related types with biflagellate zoospores are included in the family Woroninaceae. *P. inflatum* and the present parasite would most fittingly be placed in it. The family includes four genera viz. *Pseudolpidium*, *Olpidiopsis*, *Rozella* and *Woronina*. Their characteristic features are: (1) thallus plasmodial, mingling freely with the protoplasm of the host and not producing a mycelium; (2) parasitic and completely within the host; (3) sporangia multispored; (4) zoospores laterally biflagellate; (5) thick-walled resting spores in the host. The two fungi under consideration show all these features except (5). They differ from the members of the other genera in their sporangial formation. The sporangia are formed singly, and each completely fills the swollen hyphal tip of the host, and its wall is fused with that of the host and is indistinguishable from it. In the genera *Pseudolpidium* and *Olpidiopsis* the sporangia lie loosely in the host hyphae, and in the genera *Rozella* and *Woronina* the sporangia form a linear series separated by cross walls. If the sporangial form and fusion of walls constitute a generic difference, then a new genus must be erected to house the two species under consideration. The question remains whether this is advisable while the resting spores are still unknown.

If the parasite produces no resting spores it must continue its life either by reinoculation of the host, or by prolongation of the zoospore stage. The former seems to be more probable though more precarious. It was noticed in inoculation experiments that the vigorous hyphae were soon covered with swarms of attached zoospores. If, however, the host is as extensively parasitized in nature as it is in culture, being almost entirely transformed into parasitic sporangia, no such reinoculation would be possible. It is interesting to note here that in the inoculation experiments the introduction of the parasite seemed first to induce the production of normal host sporangia. This would ensure the provision of new young host plants for the subsequently produced zoospores of the parasite. Fischer (1882) observed instances of *Rozella* where a parasite did not interfere with the normal life of the host, normal sporangia and zoospores being produced, and it was only when secondary sporangia were forming that the parasite gained the upper hand. This seems to be a similar phenomenon though Fischer did not attach any significance to it.

If there is a prolongation of the zoospore stage it may be either as a zoospore or as a cyst. Many of the zoospores were seen to encyst; others continued their activity for twenty-four hours or more without abatement. Their subsequent history was not followed but it has often been observed that among bacterial colonies on bait from the river, there are small zoospore-like organisms strongly re-

sembling those of Chytrids. It is probable that water moulds both saprophytic and parasitic may be able to exist as unicells for considerable periods.

This account formed part of a thesis on the water moulds of the Hogsmill River submitted for the M.Sc. degree at the University of London, 1939. The work was carried out partly in the Royal Holloway College Botanical Laboratory, and my sincere thanks are due to Miss E. M. Blackwell, M.Sc., for facilitating this research and for her help and advice. I wish to thank Dr Ashby of the Imperial Mycological Institute for suggesting the affinities of the parasite, and to Sir Edwin Butler for his sympathetic interest and advice relating to the taxonomic position of this organism.

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HOST PLANTS OF THE BROWN ROT FUNGI IN BRITAIN

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(With Plates I and II)

In Europe, including the British Isles, the Brown Rot diseases of fruit trees are caused by two species of fungi, *Sclerotinia fructigena* Aderh. & Ruhl. (*Monilia fructigena* Pers.) and *Sclerotinia laxa* Aderh. & Ruhl. (*Monilia cinerea* Bon.).* The perfect (ascigerous) stage of these fungi is rarely found; that of *Sclerotinia fructigena* has not yet been recorded in Britain, while that of *S. laxa* has been found only once in this country (Wormald, 1921). It is thus a convenience to refer to these fungi by the names given to the imperfect (*Monilia*) stage, as it is this stage which is invariably found on infected trees. The *Sclerotinia* stage, on the few occasions when it occurred, developed on mummied fruit that had been lying on the ground for some months.

It has been usually assumed by continental workers that *Monilia fructigena* is almost confined to the pome fruits and *M. cinerea* to the stone fruits. In a recent paper by Mittmann (1938) this is again stated but with the reservation that the two species are not sharply specialized to those hosts. From observations in Britain it would be more rational, in distinguishing the two fungi by their mode of infection, to say that *M. cinerea* attacks the flowers of both pome and stone fruit trees and that *M. fructigena* is responsible for most of the Brown Rot of the fruit. It should be noted, however, that infection of the fruit of species of *Pyrus* by *M. cinerea* does occur but is rare; while on species of *Prunus*, although much of the fruit Brown Rot is caused by *M. cinerea*, the fungus most generally found, even on the common stone fruits (plum, cherry, peach) is *M. fructigena*. Blossom Wilt, so far as observations in Britain go, is invariably caused by *M. cinerea* both on the pome fruits and stone fruit trees.

Monilia cinerea on pome fruit trees

Blossom Wilt of apple trees, caused by *M. cinerea* forma *Mali*, is common and very destructive; it has been described in detail in former papers (Wormald, 1917). Blossom Wilt of pears is much less frequent, but it has been found in three localities (Wormald, 1930). The occurrence of *M. cinerea* on other species of *Pyrus* is described later in this paper.

* For a general account of these fungi see *Bulletin* no. 88 of the Ministry of Agriculture and Fisheries (Wormald, 1935).

Infection of the fruits of apple, pear and quince by *M. fructigena* is common and widespread and, by comparison, the corresponding damage by *M. cinerea* is rare. I have found *M. cinerea* on apples on three occasions only. It was seen on a single apple in the fruit shed at the Wye Agricultural College in 1920, and in 1922 two apples were found infected with this fungus. Since that time it has been found on a single apple at East Malling, but accompanied, on the same fruit, by *M. fructigena*. It has also been seen twice on small fruits (about 1 cm. long) of pear, in 1915 at Ash, in East Kent, and in 1921 on a specimen received from Exeter; numerous grey *Monilia* fructifications were present on both, and typical cultures of *M. cinerea* were obtained from the conidia.

It has been found once on quince; in 1925 a mummied flower was seen on a tree at East Malling with fructifications of *M. cinerea* on the flower and on its pedicel. In 1920 it was found on a mummied flower and on a withered leaf of medlar at Rodmersham, Kent.

Monilia fructigena on stone fruits

That *M. fructigena* is far from being confined to the pome fruits came to my notice some twenty years ago when, on a visit to a nursery in Sussex, I saw a number of plums infected with *M. fructigena* but none with *M. cinerea*. An examination of the plums in the fruit plantation at the Wye Agricultural College about that time also suggested that *M. fructigena* was quite as destructive to plums as *M. cinerea*, so fifty infected plums were taken at random and of these twenty-nine bore *M. fructigena*, thirteen had *M. cinerea* and on eight both fungi were present. On a Purple Egg plum tree seriously infected (about 15 % of the crop of that tree) 120 bore *M. fructigena*, 166 *M. cinerea* and forty-six had both; there was thus a slight preponderance of *M. cinerea* in this instance.

In more recent years observations at East Malling have shown that *M. fructigena* is generally more prevalent on stone fruits than *M. cinerea*. In 1926 *M. fructigena* was common on certain varieties on the Station. One St Julien plum tree in the "Museum Plot" bore a heavy crop of fruit, most of which were affected with Brown Rot. The fungus responsible for the rot was *M. fructigena* only; *M. cinerea* was not found on this tree. It was estimated that at least 90 % of the fruit was infected. One branch bore twenty-nine plums, and twenty-eight of these showed fructifications of *M. fructigena*; another branch had seventeen fruits, all infected (see Pl. II, fig. 6).

The preponderance of *M. fructigena* over *M. cinerea* on plums that year was seen in other instances. Of forty plums obtained from the packing shed (not specially selected, but fruit discarded by the packers as showing rot) thirty-seven bore *M. fructigena* only; the other

three bore both *M. fructigena* and *M. cinerea*. Again, on a tree of Magnum Bonum plum, eighteen showed Brown Rot of which sixteen bore *M. fructigena* and two *M. cinerea*. On a number of Cherry Plum and Morello cherry trees at Maidstone Brown Rot of the fruit was caused by *M. fructigena* only.

In 1927 also, Brown Rot of stone fruit at East Malling was caused almost solely by *M. fructigena*. In July, Morello cherries (fruit) on a trial plot at East Malling were infected with *M. fructigena* only; on two Morello trees in a Maidstone garden *M. cinerea* was found on one fruit only; all others with Brown Rot bore *M. fructigena*. During the same month Mr N. H. Grubb informed me that fully 50 % of the fruit on a St Julien plum tree in his garden was infected with Brown Rot caused by *M. fructigena*. Other plums of various varieties were examined with the result that, out of 234 with Brown Rot, 226 were found to be infected with *M. fructigena*, six with *M. cinerea* and two with both. On Black Bullace trees 254 fruits were infected and all bore *M. fructigena*.

The fruit of the varieties of plum included under *Prunus insititia* appears to be very susceptible to infection by *M. fructigena*. Severe infection of St Julien plums and Black Bullace is mentioned above. On damsons no special observations have been made in the field though both the Brown Rot fungi are known to infect the ripening fruit. On damsons in cold store, counts have been made and again both fungi were found to be responsible for considerable wastage, with, on the whole, *M. fructigena* predominating (Wormald & Painter, 1935, 1937). In 1939, clusters of infected fruits (up to twelve in a cluster) were seen on a tree of Shepherd's Bullace on the Station; more than seventy infected fruits were counted and only four of these bore *M. cinerea*; the rest were infected with *M. fructigena*. Two other trees of the same variety had fewer infected fruits, about twenty in all, but all bore *M. fructigena*.

On Morello cherries *M. fructigena* is the fungus usually associated with rotting of the ripening fruit; sometimes the infection is accompanied by an exudation of gum at the base of the stalk of an infected fruit, indicating that the fungus had first attacked the fruit and then extended within the stalk into the twig bearing it to produce a lesion.

On the fruit of peach and nectarine trees both species of *Monilia* occur, but no estimate of their relative importance in this connexion has been made, although on one occasion *M. fructigena* was noted as the only fungus causing Brown Rot of the fruit of a few trees growing under glass.

The observations recorded above show that *M. fructigena* causes quite as much rot of stone fruit as *M. cinerea* and often it is the species most generally found.

The Brown Rot fungi on other host plants

It may not be generally known that in Britain the Brown Rot fungi attack plants other than the commonly cultivated fruit trees. Many species of the genera *Pyrus* and *Prunus* are grown in this country as ornamental shrubs, and some of these have been found to be susceptible to Brown Rot infection. Possibly others are equally susceptible but have not yet become infected from other host plants, or they may have been infected and the damage not recognized as caused by a Brown Rot fungus, for the fungi do not always produce fructifications on the parts infected. The infection of ornamental shrubs is mostly by *M. cinerea*, which enters by the flowers, producing Blossom Wilt, and then grows into the twigs; if these are girdled by the resulting lesions the parts terminal to the lesions wilt. When this occurs on the young twigs, as so often happens, the condition is sometimes referred to as Twig Blight. The following instances of Brown Rot infection of ornamental shrubs have come to my notice.

Prunus serrulata Lindl.* (a Japanese Flowering Cherry). In 1925 a large tree of this Japanese ornamental cherry in a garden at Benenden, Kent, had many of the tips of the branches killed and there were definite lesions on them. The areas where the lesions occurred had borne flowers and it was inferred that infection had entered through the flowers. No fungal fructifications were seen, but *M. cinerea* was isolated in culture from the tissues of the lesions.

Similar dying-back of the branches was seen the following year and again *M. cinerea* was isolated from the lesions on the dead twigs.

Prunus tomentosa Thunb. (a Chinese Flowering Cherry). This species of flowering cherry appears to be very susceptible to Blossom Wilt and the subsequent death of the young twigs. The dead twigs give rise to grey *Monilia* fructifications the following spring.

In 1929 specimens were received from Meopham, Kent, taken from a tree severely infected. Many of the tips of the branches were withering for a length of three to twenty inches (Pl. I, fig. 4). There were also dead leafless twigs bearing pustules of *M. cinerea*; these had evidently been infected the previous year.

The flowers when first examined bore no fructifications, but on keeping wilted twigs in a moist chamber for twenty-four hours some of the dead flowers bore tufts of conidial chains of *M. cinerea*.

In 1931 dead twigs bearing withered flowers were found on bushes on the Research Station and in a private garden at East Malling. No conidial fructifications were seen, even after specimens were kept in a moist chamber for several days, but *M. cinerea* was easily isolated from such material by plating out small pieces of the infected bark.

* There are several varieties of *Prunus serrulata* in cultivation. The particular variety affected was not ascertained.

In 1939 Twig Blight, as a result of blossom infection, again appeared on the same host in a garden at East Malling. As before, no fructifications were present on the specimens examined but the fungus was isolated in culture from tissues of the twig lesions; later this strain from *Prunus tomentosus* was inoculated into Morello cherries, and fructifications of *M. cinerea* developed within three days.

Prunus pumila L. (Sand Cherry or Dwarf American Cherry). This species also is very susceptible to blossom infection with subsequent death of branches bearing infected flowers.

In 1924 a young tree in the "Museum Plot" at East Malling, had all the branches bearing flowers killed back apparently by infection through the flowers, for those branches not bearing flowers were unaffected. No fungus fructifications were seen on the flowers, but *M. cinerea* was isolated from the bark of a lesion on one of the branches.

Prunus Padus L. (Bird Cherry). In July 1931 and 1932 trees on the East Malling Research Station showed withered twigs and dead flowers (Pl. I, fig. 5). No fungus fructifications were seen but on keeping specimens in a moist chamber for three days fructifications of *M. cinerea* appeared. The fungus was isolated from the conidia so obtained and also from the tissues of dead twigs after surface sterilization. The cultures produced growth typical of *M. cinerea*.

Infection apparently occurred through the flowers. Only some of the flowers on certain inflorescences were killed; in others, however, infection extended into the axis of the inflorescence so that all the flowers withered, and sometimes into the twig bearing the inflorescence, thus killing the terminal portion of the twig.

Prunus Amygdalus Stokes (Almond). *M. fructigena* infects the fruits, and sometimes clusters of the mummified fruits are conspicuous in autumn after leaf-fall. In 1934, specimens showing this condition were received from Croydon, and it has been seen in other localities. Possibly the flowers become infected but there appears to be no record of Blossom Wilt of the common almond in Britain.

Prunus nana Stokes (Dwarf Russian Almond). A dead twig from a bush of Dwarf Russian Almond was received from Horsted Keynes, Sussex, in June 1932. *M. cinerea* was isolated from the discoloured bark. Infection had probably arisen through the flowers.

Pyrus purpurea Hort. (a Flowering Crab). Blossom Wilt of this handsome flowering crab was seen on specimens received from Seddlescombe, Sussex, in 1935.* On the recently killed inflorescences were grey *Monilia* fructifications; they were found on the flower stalks, the calyx, and the filaments of the stamens. The specimens included portions of old spurs, killed by infection during the previous year, and these also bore grey *Monilia* fructifications.

* Specimens kindly sent by Mr G. C. Johnson, Horticultural Superintendent, East Sussex.

The conidia on the old spurs measured 10–16 × 8–10μ; those on the flower stalks of the recently killed flowers were larger, measuring 14–22 × 12–16μ. This discrepancy in the size of the conidia produced on the old dead wood and on the recently infected flowers has been observed on other host plants infected with *M. cinerea*.

Cultures prepared from (*a*) conidia from an old spur, (*b*) conidia from a flower stalk of flower infected that year, and (*c*) the tissues of the axis of a young infected spur, all gave rise to cultures typical of *M. cinerea*.

The same year a similar Blossom Wilt of the same host was seen in a garden at East Malling. In 1937, specimens received from Lyndhurst, Hampshire, showed what was apparently Blossom Wilt; no *Monilia* fructifications were present but *M. cinerea* was isolated in culture from the tissues of one of the twigs, and inoculations of the strain isolated into plums produced a rapid rot, and fructifications of *M. cinerea* appeared.

In 1935, the fruit of this crab was infected with *M. fructigena* on trees at Reading (Berkshire) and at East Malling.

Pyrus elaeagnifolia Pall. (a Wild Pear from Asia Minor). Typical Blossom Wilt and canker was seen in 1925 on a Caucasian Pear Tree growing on the East Malling Research Station. The end of a branch was dead for a length of seven inches; at the lower end of this portion there was a girdling canker two inches long with a dead spur near the middle; one flower of the spur bore pustules of *M. cinerea* so that it was assumed that infection had started at this flower, and that the fungus extended into the spur and then into the branch to cause the canker.

Pyrus Aria Ehrh. (White Beam). In June 1924 infection of flowers was seen on a White Beam tree in the "Museum Plot" at East Malling Research Station. The infected inflorescences were not wholly destroyed but portions were killed and grey *Monilia* fructifications were present on some of the flowers and pedicels (Pl. I, fig. 1). The morphological and cultural characters of the fungus corresponded to those of *M. cinerea*.

Pyrus japonica Thunb. (Japanese Quince). In a garden at Maidstone, in June 1917, a Japanese Quince, growing on the side of the house, was seen to have wilted clusters of flowers with cankers round the base of some of the dead inflorescences (Pl. I, fig. 2). Grey *Monilia* fructifications were present on some of the wilting flowers. The dimensions of the conidia and the habit of the cultures isolated from conidia were those of *M. cinerea*.

A bush of "Japonica" in an East Malling garden showed severe Blossom Wilt and Twig Blight in June 1939. No *Monilia* fructifications were seen on the flowers but culture plates prepared from the tissues of the lesions on twigs gave growth typical of *M. cinerea*, and inoculations into green Morello cherries (fruit) produced a rapid rot, and fructifications of *M. cinerea* appeared within three days.

Cross-inoculations

It is important to realize that probably all the host plants mentioned, fruit trees and ornamental bushes alike, serve as sources of infection for the others, for there is little evidence that biologic forms occur in the Brown Rot fungi. During the course of this investigation considerable variation in cultural characters has been observed in the strains isolated of both fungi, even among strains from one species of host. Pesante (1935, 1937) has observed similar variation in cultures of the Brown Rot fungi in Italy and refers to biologic forms or races on those grounds. Such cultural forms are known to exist in many species of fungi and they bear little or no relation to specialization of parasitism within the species.

The Blossom Wilt of the apple in Britain is caused by a form of *M. cinerea* biologically distinct from that of the stone fruit trees since strains from the latter failed to produce typical Blossom Wilt of apple in inoculation experiments (Wormald, 1917); these results were confirmed by Boyle *et al.* (1928) in Ireland, though Christoff (1938) finds no such distinction in Bulgaria. In other cross inoculations, described below, successful infection has been obtained. Mittmann (1938) also describes success in a number of cross inoculations on various hosts, with isolations of both *M. fructigena* and *M. cinerea.*

I have carried out a number of such cross inoculations from time to time and a summary of the results is here given.

Monilia fructigena

(1) Quince to apple. Apples inoculated with a pure culture from quince became brown, then black (the condition known as Black Apple).

(2) Apple to plum. Conidia taken direct from an apple were inoculated into plums (var. Shepherd's Bullace) which rapidly became infected and produced fructifications of *M. fructigena* within three to four days.

(3) Plum to apple and pear. Inoculations were made with conidia taken direct from a plum. Rapid rot set in and within seven days the whole surface was brown and bore numerous fructifications of *M. fructigena.*

Monilia cinerea

(1) Pear (spur) to apple (flowers). Typical Blossom Wilt resulted but only in one inflorescence out of six; the experiment has not been repeated.

(2) Pear (spur) to plum (fruit). Inoculations on trees in the open produced rapid fruit rot, and fructifications of *M. cinerea* appeared within five days.

(3) Medlar (leaf) to apple (flowers). Typical Blossom Wilt.

(4) Plum (twig) to pear (flowers). Typical Blossom Wilt.
(5) Plum (fruit) to Morello (flowers). Typical Blossom Wilt.
(6) Cherry (fruit) to Morello (flowers). Typical Blossom Wilt.
(7) Cherry (fruit) to pear (flowers). Typical Blossom Wilt.
(8) Apricot (twig) to cherry (fruit). Rapid rot of fruit inoculated, and the rot then extended to others of same cluster.
(9) Apricot (twig) to cherry (flowers). Inoculated flowers wilted (Fig. 9).
(10) *Prunus tomentosa* (twig) to apple (fruit). Rapid rot with appearance of fructification of *M. cinerea* within four days.
(11) *Prunus tomentosa* (twig) to pear (fruit). Ditto.
(12) *Prunus tomentosa* (twig) to Morello (fruit). Ditto.
(13) *Pyrus japonica* (twig) to apple (fruit). Ditto.
(14) *Pyrus japonica* (twig) to pear (fruit). Ditto.
(15) *Pyrus japonica* (twig) to Morello (fruit). Ditto.
(16) *Pyrus purpurea* (twig) to plum (fruit). Rapid rot with fructifications within seven days.

Corresponding inoculations with isolations from fruit trees have not been made on flowering shrubs. Until such experiments have been carried out it is to be assumed however (in view of the ready infection of fruits, using isolations from three ornamental shrubs), that fruits bearing *M. cinerea* are a potential source of infection for the flowers of those species of *Pyrus* and *Prunus* that are cultivated in gardens for their beauty.

In efforts to reduce the severe losses resulting from infection by the Brown Rot fungi all possible sources of infection should be borne in mind, and hygienic measures by the removal and burning of all infected parts should be practised whenever possible. Such measures have frequently been emphasized with reference to fruit trees, but it must be recognized that ornamental trees too may become infected and the necessary steps should be taken to keep these also free from Brown Rot diseases, especially when, as in nurseries, ornamental bushes and fruit trees are grown in close proximity.

Summary

Of the two Brown Rot fungi found in Britain *Sclerotinia laxa* (*Monilia cinerea*) is the cause of Blossom Wilt of fruit trees and ornamental shrubs of species of *Pyrus* and *Prunus*, while *Sclerotinia fructigena* (*Monilia fructigena*) is the fungus most frequently found associated with fruit Brown Rot.

Observations of the occurrence of *M. cinerea* on core fruits, and of *M. fructigena* on stone fruits are described.

The fungi have been found on a number of species of ornamental shrubs.

Cross-inoculations with the fungi from various hosts have yielded positive results on a number of other hosts.

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EXPLANATION OF PLATES I AND II

Plate I

Fig. 1. Inflorescence of White Beam with about half the flowers infected with *Monilia cinerea*.

Fig. 2. Infected flowers of *Pyrus japonica*.

Fig. 3. Blossom infection of *Pyrus purpurea* with accompanying Twig Blight.

Fig. 4. Twig Blight of *Prunus tomentosa*.

Fig. 5. Twig Blight of *Prunus Padus*.

Plate II

Fig. 6. St Julien plums with *Monilia fructigena*.

Fig. 7. Blossom Wilt and Twig Blight of Morello Cherry after inoculation of the flowers with *Monilia cinerea* from plum.

Fig. 8. One cherry was inoculated with *M. cinerea* from apricot, and the rot is extending to others in contact with it.

Fig. 9. On the left below are two wilting flowers that were inoculated with *M. cinerea* from apricot.

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Fig. 1

Fig. 2

Fig. 3

Fig. 4

Fig. 5

Fig. 8

Fig. 9

Fig. 7

Fig. 6

NOTE ON THE DISTRIBUTION OF BASIDIA IN FRUIT BODIES OF *NYCTALIS PARASITICA* (BULL.) FR.

By C. T. INGOLD

(With 3 Text-figures)

Nyctalis parasitica, one of the few agarics parasitic on other agarics, is of special interest because the fruit body sometimes bears two kinds of spores, chlamydospores, formed within the tissue of the gill, and basidiospores.

Most of the details of the life history of the fungus were made clear by Brefeld (1884) who succeeded in germinating both basidiospores and chlamydospores.

De Bary (1859) investigating *N. parasitica* never found basidia in any of the fruit bodies which he examined. Brefeld (1884) found occasional basidia in some fruit bodies. Buller (1924), who gives a full history of the work of other investigators on *N. parasitica*, adds his own observation that fruit bodies examined by him were sterile. He concludes that basidia production in this fungus must be regarded as very exceptional. Recently Thompson (1936) in America has grown the fungus saprophytically in pure culture. He made a careful examination both of fruit bodies occurring in nature and those produced in culture, but he failed to find basidia.

In Swithland Wood, six miles north of Leicester, I have found *N. parasitica* growing abundantly as a parasite on *Lactarius vellereus*. In the part of the wood where *L. vellereus* was common most of the fruit bodies had a crop of *Nyctalis parasitica*. A large number of the fruit bodies of the parasite were examined in August 1938, and nearly all these bore basidia. Observations were again made a year later, when every fruit body examined (over fifty) was fertile. The fruit bodies varied from small ones with a cap less than 1 cm. in diameter up to large ones, 2·5 cm. across. From the fruit bodies normal basidiospore-prints were obtained, which, however, were much fainter than is usual with white-spored agarics of similar size. Nevertheless, a spore print clearly visible to the unaided eye was usually obtained after a pileus had been inverted over a glass plate for four hours. The spores in these prints, when examined in water, agreed in size with the measurements given by Rea (1922).

Sections of the pileus, cut vertically and more or less tangentially, showed the gills covered with a layer homologous with the normal

hymenium of Hymenomycetes. Most of this layer, however, was sterile. This "sterile hymenium" differed from the normal hymenium not merely in the absence of basidia. It consisted of filamentous elements nearly twice as long as the paraphyses of the fertile hymenium, and these elements were fairly loosely arranged, not closely pressed

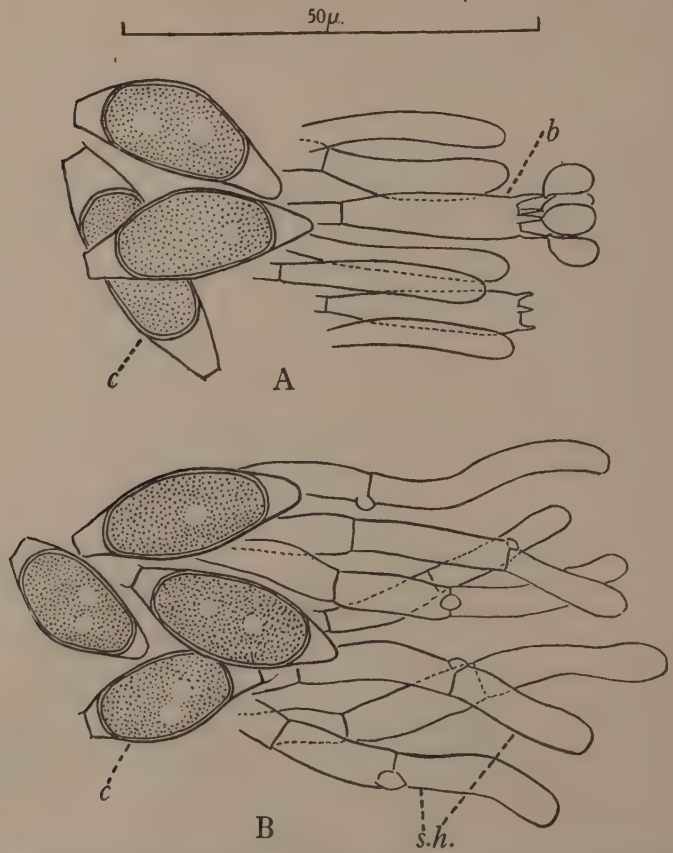

Fig. 1. *Nyctalis parasitica*. Details of fertile hymenium (A) and "sterile hymenium" (B). *b*, basidium; *c*, chlamydospore; *s.h.* hyphae of "sterile hymenium".

together, as in a palisade, like the elements of the true hymenium (Fig. 1 B). The fertile hymenium was very much like that of any normal toadstool (Fig. 1 A). Below both kinds of hymenium the tissue of the gill was largely composed of a mass of chlamydospores.

The distribution of sterile and fertile hymenia on the gills followed a definite plan. True hymenium with basidia occupied the free edge

of each gill and usually extended from this edge on to the lateral surfaces of the gill (Fig. 2), but it soon gave place to "sterile hymenium". The boundaries between the two kinds of hymenium were nearly always quite sharp. Frequently the fertile hymenium was entirely limited to the free edge of the gill and did not extend on to the vertical gill surfaces. Occasionally in a sporophore a few of the smaller, shallower gills were found to have no true hymenium.

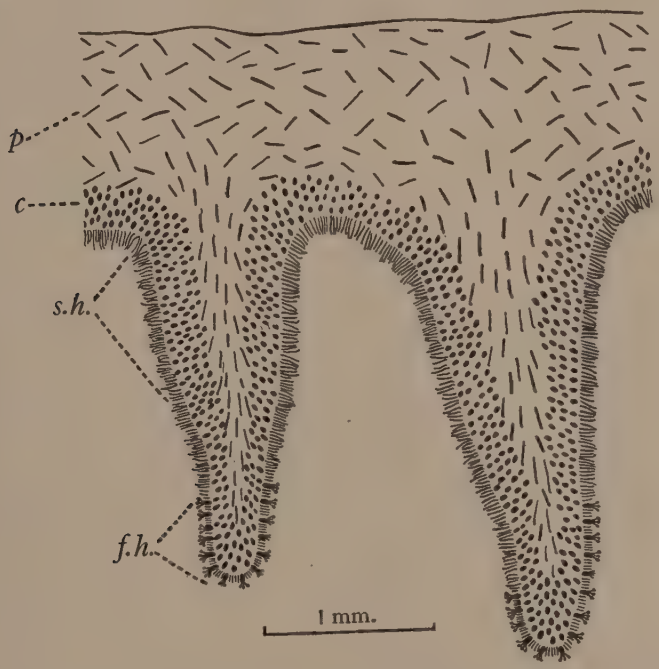

Fig. 2. *Nyctalis parasitica*. Diagram showing the distribution of tissues in a vertical tangential section of the pileus. Outlines of the tissues drawn with the aid of a *camera lucida*. *c*, zone of chlamydospores; *p*, pileus tissue; *f.h.* fertile hymenium; *s.h.* "sterile hymenium".

When a gill was removed from a fruit body and examined in surface view by reflected light under the low power of the microscope, the distinction between true hymenium and "sterile hymenium" was very clear. The "sterile hymenium" had a whitish fleecy appearance, while the true hymenium was greyish with a translucent and almost water-soaked appearance (Fig. 3).

In *N. asterophora*, the only other British species of *Nyctalis*, the chlamydospores are produced, not in the tissue of the gill as in *N. parasitica*, but in the tissue of the upper region of the pileus. The

stellate chlamydospores finally form on the cap a dry powder which can be blown away by the wind. In the specimens of *N. parasitica* which I have examined, the gills, with the smooth chlamydospores immersed in the subhymenial tissues, never break down to a dry

Fig. 3. *Nyctalis parasitica*. Longitudinal section of a fruit body showing two gills. On each the "sterile hymenium" is stippled and the fertile hymenium is shown by vertical shading, ×2.

powder, and probably can be liberated only when the fruit body decays.

It would be interesting to know whether *Nyctalis parasitica* in this country is usually sterile, or whether the kind of fruit body which gives a spore print is common.

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TUBERCULARIA

By T. PETCH

THE genus *Tubercularia*, as accepted at present, was established by Tode (1790) with the species, *T. vulgaris*, *T. fasciculata*, *T. volvata* and *T. sulcata*. He divided *T. vulgaris* into two forms, *subsessilis* and *stipitata*, but withdrew that in 1791 as superfluous. Of the other species, *T. volvata* and *T. sulcata* were referred to *Ditiola* by Fries (1823), while Persoon (1822) placed *T. fasciculata* as a variety of *Peziza carpinea*, but said it seemed to be a distinct species (of *Peziza*).

Persoon (1796) added another species, *T. discoidea*, and in 1801 he included in the genus, *T. discoidea* Pers., *T. vulgaris* Tode, *T. granulata* Pers., *T. confluens* Pers., and *T. Castaneae* Pers. In 1803, Schumacher described nine new species, *T. Artemisiae*, *T. Pini*, *T. minuta*, *T. Pruni*, *T. Cerasi*, *T. Populi*, *T. sulcata*, *T. nigra* and *T. hirsuta*. Link (1825) stated that it was not possible to determine Schumacher's species because his collection had been destroyed in the siege of Copenhagen in 1807, but, following Fries (1832 and Index), it is usual to regard *T. Artemisiae* as *T. vulgaris*, and *T. Cerasi*, *T. nigra*, *T. Pini*, *T. sulcata* and *T. hirsuta* as not *Tubercularia*. *T. Pruni* and *T. Populi* are given by Saccardo (1886) as synonyms of *T. vulgaris*.

Albertini & Schweinitz (1805) described a new species, *T. ciliata*, and two others, *T. saligna* and *T. bicolor*, about which they had some doubt. *T. ciliata* A. & S. is now *Volutella ciliata*. Link (1825) discarded the other two with the remark that their authors themselves regarded them as doubtful species, but Wallroth (1833) renamed *T. saligna*, *T. granulata* var. *Salicis*. Fries (1815) described five new species as *T. Acaciae*, *T. sarmentorum*, *T. Menispermi*, *T. herbarum* and *T. liceoides*, and in the following year, Link (1816) added *T. ciliata* Link and *T. floccosa* Link. The latter species had been sent him by Nees, who himself published it (1817) as *T. velutipes*. Similarly, *T. ciliata* Link is the same as *T. ciliata* Ditm. (1817).

The genus had expanded at a rapid rate, usually by the addition of new species based on differences of host; and in 1825, Link made the first attempt to reduce it to order. He enumerated the following species, with their synonyms.

T. vulgaris Tode. *T. lutescens* Link. *T. minor* Link; syn. *T. Acaciae* Fr., *T. Castaniae* Pers., *T. confluens* Pers., *T. discoidea* Pers., *T. mutabilis* Nees. *T. granulata* Pers.; syn. *T. Pseud-acaciae* Rebent. *T. dubia* Link, a re-naming of the American species, *T. nigrescens* Schwein. *T. floccosa* Link; syn. *T. velutipes* Nees, *T. nigricans* Link, Bulliard, pl. 455,

fig. 1. *T. ciliata* Ditm., *T. liceoides* Fr., *T. herbarum* Fr.; syn. *T. Artemisiae* Schum., *T. Menispermi* Fr.

In *Systema Mycologicum*, Fries (1832) included *T. vulgaris* Tode, *T. ciliata* Ditm., *T. herbarum* Fr., *T. granulata* Pers. and *T. nigricans* Link, with *T. liceoides* Fr. as a state of *T. granulata*, but referred his readers to Link (1825) for the remaining species, thus providing numerous problems for nomenclature which begins with Fries, *Systema*. He did, however, mention *T. minor* Link in his observations on the genus; and in the Index he gave *T. Acaciae* Fr., *T. Castaneae* Pers., and *T. discoidea* Pers., as synonyms of *T. minor*, and *T. Artemisiae* Schum. and *T. confluens* Pers., as synonyms of *T. vulgaris*. In addition, the Index includes a number of species which had been described as *Tubercularia* but had been transferred to other genera and need not be detailed here.

Wallroth (1833) made another attempt to clarify what he styled "*genus vexatum*", principally by reducing species to varieties. He enumerated four species, *T. vulgaris* with seven varieties, *T. granulata* with eight varieties, *T. liceoides* Fr. and *T. ciliata* Ditm. Apparently his work was written before the completion of Fries, *Systema*, as it does not take into account Fries's withdrawal of *T. liceoides*. His varieties are based principally on host differences, and he appears to have drawn his conclusions from the host records.

Corda (1829) described and figured *T. floccipes*. Subsequently he dealt extensively with the genus, describing and figuring *T. carneola* Cda., *T. carpogena* Cda., *T. rufa* Cda., *T. effusa* Cda., *T. fusisporum* Cda., *T. pinophila* Cda., *T. Sambuci* Cda., *T. herbarum* Fr., *T. liceoides* Fr., *T. minor* Link var. *rosea*, *T. mutabilis* Nees, *T. confluens* Pers., *T. granulata* Pers., *T. hysterina* Cda., *T. Aesculi* Opiz, *T. vulgaris* Tode, *T. vulgaris* var. *Rubi* Rabh., *T. vaginata* Cda., and *T. carnea* (Cda.) Sacc., in 1837; *T. purpurata* (Cda.) Sacc., *T. granulata* var. *cava* Cda., and *T. volutella* Cda., in 1838; and *T. Pinastri* Libert in 1839.

Fries (1849) enumerated for Scandinavia, *T. vulgaris* Tode, with *T. discoidea* Pers., as a variety, *T. confluens* Pers., *T. corrugata* Fr. (*nomen nudum*), *T. granulata* Pers., *T. liceoides* Fr., *T. mutabilis* Nees, *T. expallens* Fr. (*nomen nudum*), *T. ciliata* Ditm., *T. sarmentorum* f. *Rubi*, *T. Pinastri* Libert and *T. herbarum* Fr. It will be noted that Fries revived *T. liceoides* as distinct from *T. granulata*.

Tulasne (1865) stated that he considered as more or less aberrant forms of *T. vulgaris*, but not as distinct species, *T. nigricans*, *T. discoidea*, *T. granulata*, *T. confluens*, *T. Castaneae*, *T. Menispermi*, *T. sarmentorum*, *T. minor*, *T. mutabilis* and *T. expallens*—a view with which Saccardo (1886) said he willingly agreed.

In the first half of the last century, species of *Tubercularia* had been founded on macroscopic characters and host differences; and as the European species are variable and not restricted to a single host, it

is to be expected that most of the earlier names relate to two or three species only. The first attempt to differentiate between them on microscopic data was made by Paoletti (1887), who examined 126 specimens, supposed to include twenty-six species and several forms, in the herbarium of Prof. P. A. Saccardo, most of which had been issued in well-known European exsiccata. These he reduced to ten species, three of which were new.

Paoletti first separated those species in which the conidia are borne only on the apex of the conidiophore; in this group he had only two species, *T. versicolor* Sacc. and *T. Libertiana* Paol., which really are not co-generic with *T. vulgaris*. To divide the remaining mass, he took the length of the stalk, the colour of the stroma, and the branching of the conidiophore.

As regards the stalk, it will be evident to anyone who collects *T. vulgaris* or *T. minor* in quantity that this character is variable. In some sporodochia the stalk is short and almost completely immersed in the host, so that the sporodochium appears sessile, but in other specimens in the same gathering, the stalk may be much longer and emergent, so that the sporodochium is distinctly stalked.

Paoletti did not record how he judged the colour of the stroma, as distinct from the colour of the spore-mass, whether the colour of the head after removal of the conidia, or the external colour, or the internal colour as seen in section. All these may change with age, and their appearance in herbarium specimens may depend on the stage of development of the sporodochium when collected.

In *T. vulgaris*, the conidia are borne apically on the conidiophore and on short lateral branches. Paoletti found that, in some of the alleged species which he examined, the lateral branches were short, not exceeding the conidium in length, while in others some branches of some conidiophores were longer than the conidia and sometimes again branched. Accordingly he adopted that as a specific difference, and based the ultimate separation of his species on whether they had all the branches of the conidiophores equal to or shorter than the conidium, as in *T. vulgaris*, or whether *some* conidiophores had one or more branches longer than the conidium, as in *T. minor*. When I began this investigation, that criterion appeared to me to be valid, but as more specimens were examined, it became evident that it was unreliable. In sporodochia referable to *T. minor*, conidiophores with long branches are common; in those referable to *T. vulgaris* they are not obvious, but can generally be found by careful searching. Moreover, conidiophores with branches longer than the conidium can often be found in sporodochia which, from the development of *Nectria cinnabarina* on the same or adjacent stromata, can only be regarded as *T. vulgaris*, while the perithecia which occur on stromata which have all the characters of *T. minor* are those of *N. cinnabarina*.

Consequently, it is not possible to separate *T. minor* from *T. vulgaris* on the length of the stalk, the colour of the stroma, the presence of conidiophores with long branches, or a difference in the perithecial stage. I have therefore been compelled to agree with Tulasne and Saccardo that *T. minor* is only a form of *T. vulgaris*. It probably owes its morphological differences, which are differences of degree only, to its looser structure, though I am unable to offer any explanation of its peculiar internal colour changes, which will be mentioned later.

Cultures have been attempted only on oatmeal agar. No difference was observed between the growth of *T. vulgaris* and that of *T. minor* on that medium. The cultures produced white, tomentose, pulvinate or subcylindrical stromata, but no conidiophores or conidia.

This work was undertaken with the object of identifying the commoner British species of *Tubercularia*. Attention has therefore been confined to species which have been recorded for this country, and to European species which might be expected to occur here. North American and tropical species have not been examined, and no attempt has been made to deal with the whole mass of material of this genus, over 500 collections, in the herbaria of Kew and the British Museum.

Tubercularia vulgaris Tode

In the typical form, the sporodochium consists of a pulvinate head, even or tuberculate, and a short stalk. Usually the stalk is almost completely immersed in the host, and the head is concave beneath, its margin resting on the host, so that the sporodochium appears sessile. Forms which are evidently stalked, i.e. with a projecting stalk which raises the head above the surface of the host, also occur, but frequently the stalk in such examples is sheathed for part of its length by the upturned periderm of the host, so that this variation may depend upon the structure of the host. I have observed such a stalked form on birch twigs, and Paoletti described and figured it as *T. Rhamni* on *Rhamnus*.

The appearance of the head varies with the state of development of the fungus. At first it is red and subtranslucent, and appears horny when dry, but when masses of conidia have developed it is pinkish and opaque when dry. The stalk is red or brownish red externally, sometimes becoming fuscous. Internally the layer of conidiophores and conidia is at first red and subtranslucent, but on drying it becomes deep pink, with a narrow translucent zone often persisting for some time at the base. The stroma is pale yellow or ochraceous internally when dry. I use the term stroma for all the tissue below the layer of conidiophores (including the stalk), which is apparently what Paoletti intended by that term.

The stroma is parenchymatous, composed, in the interior, of cuboid or rectangular cells, from $9 \times 6\mu$ to $27 \times 9\mu$, with hyaline walls about 2μ thick. Sometimes isolated files of rectangular cells occur, but in general the tissue is irregularly parenchymatous. The outer tissue of the stroma is composed of small cells only, about $4–6\mu$ diameter, usually with red walls, and often in files which curve outwards. A short distance below the zone of conidiophores, the irregularly parenchymatous tissue may give rise to parallel, laterally adherent files of thin-walled rectangular cells, $2–4\mu$ broad. The conidiophores are borne on the uppermost cells of the stroma, one, or two, from each cell.

The conidiophores are usually strongly curved, $1·5–2\mu$ diameter, and bear solitary conidia apically on the main conidiophore and on short lateral branches. The lateral branches are sometimes so short that the conidia appear almost sessile, but conidiophores with long lateral branches may be found, especially near the margin of the sporodochium. The conidia are hyaline, mostly cylindrical, usually curved, with some narrow oval, generally $5–9 \times 2–2·5\mu$, sometimes up to 11μ long.

Paoletti (1887) gave *T. Ribesii* West., *T. Populii* Schum., *T. Pruni* Schum., and *T. Robiniae* Kickx, as synonyms of *T. vulgaris*, and found that the type collections of *T. Berberidis* Thüm., and *T. Ailanthi* Cke., were also that species.

T. lutescens Link was said by Fries (1832*a*) to occur with *Nectria ochracea* Grev. & Fr. As the latter is a yellow form of *N. cinnabarina*, it is most probable that *T. lutescens* is *T. vulgaris*.

T. sarmentorum and *T. Menispermi* were described by Fries at the same time (1815), but later (Index) he withdrew the latter name as a synonym of the former. Fries issued specimens of *T. sarmentorum* on *Menispermum* in *Sclerom. Suec.* no. 259, and Link, after examination of one of these, stated that it did not bear a stratum of conidia, and suggested that it was an imperfect *Fusarium roseum*. Wallroth (1833) placed *T. sarmentorum* as a variety of *T. vulgaris*, and added to the description the phrase, emerging in lines longitudinally through fissures in the bark, a character which, as pointed out by Paoletti, depends upon the host rather than upon the fungus. Fries, *Sclerom. Suec.* no. 259, is *T. vulgaris*. Link's observation was probably due to the fact that some of the sporodochia in Fries's specimens have been eaten off down to the bases of the conidiophores. Thümen's specimens on *Vitis* in *Mycoth. Univ.* no. 1196 and *Pilze Weinst.* no. 24, and Rabh. *Fung. Europ.* no. 585 on *Koelreuteria paniculata* are *T. vulgaris*. Paoletti took as *T. sarmentorum* a specimen on *Begonia* twigs collected by Saccardo in Italy, a stalked specimen with an expanded base, but from his description and figures it does not differ from *T. vulgaris*. *T. sarmentorum* must be regarded, from the specimens on *Menispermum*

issued by Fries, as a synonym of *T. vulgaris*, though the first host mentioned in his description of the species is *Vitis*.

T. Rhamni Paoletti is a stalked specimen of *T. vulgaris*, from his description and from the specimen, Roum., *Fung. Sel. Gall. Exsicc.* no. 273, cited by him. *T. Rhamni* Paol., on *Rhamnus frangula* in Petrak, *Fung. Alban. et Bosn. Exsicc.* no. 161, is *T. vulgaris*.

British specimens of *T. Sambuci* Cda., and *T. Aesculi* Opiz are *T. vulgaris*.

T. aquifolia Cke. & Massee, on leaves of holly, is *T. vulgaris*. The sporodochia in the type specimen are small, with conidia, 5–8 × 2–2·5 μ. The conidiophores have been eaten off (in part), leaving lengths of about 20 μ, arising two or three together from a basal cell. That explains Cooke and Massee's statement that the conidiophores are rather thick and furcate, while their spore measurement, 12–15 × 2–3 μ, probably refers to the length of the conidiophore remaining. Where normal conidiophores are present, they are those of *T. vulgaris*.

T. conorum Massee, type in Herb. Kew., is *T. vulgaris*, with conidiophores straighter than usual.

T. Berberidis Thüm., is discussed under *T. granulata*.

Form *minor* was described as *T. minor* by Link (1825), who stated that it was smaller than *T. vulgaris*, immersed, red or white, with a very red, smooth and diffluent stratum of conidia; if the spore masses spread so that several individuals were united, it became *T. confluens*; while when effete, the conidia having entirely or partly slipped off, it became *T. discoidea*. Persoon (1801) described *T. discoidea* as hemispherico-discoid, and added that some specimens were confluent, and the head was smooth, not sulcate, the conidia being easily washed away by the rain, so that a dingy white, naked stroma remained; and *T. confluens* as gregarious, confluent, pinkish red, small, rather flat, subcircular, oblong or angular. Link gave as synonyms, *T. Castaneae* Pers., and *T. Acaciae* Fr., a view which Fries (Index) accepted. There seems no doubt that Link was right as regards *T. discoidea* and *T. confluens*, but his choice of the name *minor* was not a happy one, as this form varies in size as much as the normal form of *T. vulgaris*. The epithet *discoidea* appears from the herbarium specimens to have been applied subsequently to flat, circular sporodochia, slightly depressed in the centre, part of the spore mass having disappeared.

The sporodochia may be stalked or "sessile", the latter having the stalk almost totally immersed in the host, but when well-developed they are distinctly stalked. On *Brassica*, the stalk is almost lacking (*T. Brassicae* Libert). The head is at first pulvinate or subhemispherical, red and subtranslucent, becoming yellowish red and opaque, sometimes pinkish red when it is covered by a dry mass of conidia. It is even at first, but may become irregularly tuberculate or cracked. The conidial mass is often very viscid, so that it adheres strongly to

anything which comes in contact with it, while in wet weather it may become so fluid that, if growing on a suberect branch, it will run down over the bark, uniting with those of other sporodochia in streaks. This deliquescence makes the shape of the head very variable, and, though usually circular at first, it may become, as noted by Persoon, oblong or angular. When the conidia have been partly washed off, the head may have a white margin (*T. ciliata* Ditm.), or may be mottled with white patches. The exposed conidiophores sometimes turn red. If practically all the conidia have disappeared, the surface of the stroma is white, or sometimes red, and minutely tomentose.

Externally, the stalk is at first reddish, but ultimately it becomes white, or white with a reddish tinge. Internally, the stroma is red or purple-red and subtranslucent at first, the colour becoming paler towards the exterior, but increasing in intensity in the centre down to the base. As the stroma ages, the red colour becomes concentrated in definite regions, the remainder of the stalk becoming white. Most generally, the colour is concentrated at the base of the stalk, so that if the sporodochium is broken out of its socket, a vivid red patch is left. Sometimes it is concentrated in a transverse zone immediately below the stratum of conidiophores, which is a specific character of *T. subpedicellata* Schw.; or it may be concentrated in a central conical column, extending upwards from the base of the stalk (*T. longipes* Peyl). When the stroma has split vertically internally, the red colour may concentrate round the cavity, giving it the appearance of an embedded red perithecium in fresh specimens (*T. floccipes* Cda., and *T. vaginata* Cda.), but reddish brown and fibrillose when dry. All these variations have been observed, together with normal *T. vulgaris*, in an extensive development of sporodochia on the fallen trunk of a beech which had been blown down when living.

Although the coloration of the stroma is distinctive in fully developed, and especially in long-stalked, specimens, when fresh, it cannot be always employed to separate *T. minor* from *T. vulgaris* in dried material. If the specimens have been dried in an early stage, before the stroma has turned white, they do not become white internally, but, as in so many red, subtranslucent fungi the stroma dries pale yellow internally and externally, sometimes red at the base of the stalk. Then they are indistinguishable from typical *T. vulgaris*.

The stalk is often very thick, in comparison with the diameter of the head (*T. crassostipitata* Fuck.). Sometimes it is sheathed at the base, as though the growth of the outer tissue had failed to keep pace with that of the inner (*T. vaginata* Cda.). When old, stalked specimens may become funnel-shaped, red in the funnel, subsequently bleaching to white, with a lobed margin and sometimes a white disk of effete conidiophores in the funnel.

Internally, the stroma of form *minor* is parenchymatous, with more or less isodiametric cells at the base, but soon passing into parallel vertical files of elongated rectangular cells, especially in the centre. In stalked specimens, the outer layer of the stalk is composed of rectangular cells and is vertically fibrillose. Probably owing to its structure, the stroma appears to split vertically more readily than in typical *T. vulgaris*. Towards the upper part of the stroma, the elongated cells diminish to 6–8 μ diameter, stouter than the corresponding tissue in typical *T. vulgaris*, and the files frequently separate, so that the uppermost two or three segments are free. Two or three conidiophores arise from the apex of the uppermost cell, and, if the files have separated, from the two succeeding cells below.

The conidiophores are usually more or less straight, sometimes curved above, but rarely as strongly curved as those of typical *T. vulgaris*. They are of the same type as the latter, but *some* of them, in addition to short branches, have branches much longer than the length of a conidium and sometimes again branched. The conidia are hyaline, cylindrical, usually straight, or oblong-oval, or oval, or inequilaterally oval, sometimes wedge-shaped, 5–9 × 2–3 μ. The conidia are slightly broader than those of typical *T. vulgaris*, with a larger proportion of oval forms.

Examples of form *minor*, differing rather widely from one another, were found in December 1937 on pieces of the trunk of a walnut tree which had been blown down in May of that year and immediately sawn up and split into billets for firewood, the billets being stored in a heap under cover. One piece bore sporodochia on the outer surface of the bark, and also, the bark having been loosened, on the inner surface. The sporodochia on the exterior were "sessile", pink, crowded, with white tomentose tufts between them, or arose from white tomentose patches. Some of the heads were minutely tomentose with projecting conidiophores, and some bore projecting columns of conidiophores and conidia. The sporodochia on the inner surface of the bark were at first covered by a thin film of white mycelium, then emergent. At first sight it was thought that they had been attacked by a white Hyphomycete, but that proved to be incorrect. They were usually scattered, and distinctly stud-shaped, stalked, with an expanded discoid base, and a white, swollen, tomentose ring round the base of the stalk, which consisted of hyphae growing out more or less horizontally from the stalk. Some of these stromata also were tomentose with projecting conidiophores, but no conidiophores were found among the hyphae surrounding the base of the stalk. These examples are no doubt abnormal, owing to the peculiar situation in which they developed, but they are of interest in showing possible variations.

Sowerby's figure of *T. vulgaris* (*Clavaria coccinea*) in *English Fungi*, pl. 294 appears to be form *minor*.

T. Brassicae Libert, in Libert no. 1019, is form *minor*, as previously determined by Paoletti. *T. vulgaris* on decaying stalks of *Brassica* appears to be always form *minor*.

T. Coryli Paoletti is form *minor* from his figures and description. Paoletti described the stalk as "albido", but stated that the branches of the conidiophore were equal in length to the conidia. His figures, however, show some branches longer than the conidia, while the figures of the sporodochia show typical, stalked, confluent form *minor*.

T. Euonymi Roum., in Roum., *Fung. Sel. Gall. Exsicc.* no. 55, is form *minor*, as previously determined by Paoletti.

T. expallens Fr., was recorded by Fries, by name only, in the Index to *Systema Mycologicum*, and was listed by him again in *Summa Veg. Scand.* The description given in Saccardo (1886), "sporodochia subglobose, minute; stroma whitish, stratum of conidia rosco-pallid then yellowish; conidia ellipsoid, ends obtuse; on branches, especially of horse-chestnut in France and Belgium" was taken from Kickx (1867), who wrote "*T. expallens* Fr. in litt. ad Desm.", and cited Desm. *Pl. Crypt. France* fasc. 4, no. 172. Apparently, Desmazières had sent a specimen to Fries, who gave it a name, but did not publish a description. A specimen in Herb. Kew., Desm. *Crypt. France* Ser. 1, no. 172, named "*T. expallens* Fr. in litt.", contains weathered stromata of form *minor*, some of them attacked by a white Hyphomycete. It would appear that this must be regarded as a co-type.

T. floccosa Link (1816) was founded on a specimen sent to Link by Nees, who published another description of the same fungus in the following year (1817) under the name *T. velutipes*. According to Link, it was globose, pale red, minute, scarcely the size of a pin's head, covered above with white flocci. Nees stated that it was shortly stalked, with a rounded, even, cinnabar-red head, and a thick black, grey or white, tomentose stalk, expanded at the base into a floccose foot. Nees added that the fungus at first formed a disk of white flocci, with a blackish granular centre, under the epidermis, the flocci then growing over the blackish disk and developing into the sporodochium. In Herb. B.M., there is a specimen marked "*T. velutipes* Nees. In *Rhoe typhina*, ab auctore missa, Dr Schmidt", *ex* Herb. R. J. Shuttleworth, which agrees with Nees's description. The sporodochia are form *minor*. Where the epidermis has been removed, the host bears minute, flattened pulvinate, black cushions, greyish tomentose, with the tomentum sometimes spreading over the substratum. Internally, these cushions are fuscous, the discoloration extending into the underlying cortex, and they consist almost entirely of cortical cells, with a few projecting hyaline hyphae. There is no indication that these

cushions (? lenticels) are in any way connected with the *Tuberculariа*, and any such association must have been accidental. A specimen in Herb. Kew., from ? Desmazières, labelled "*T. velutipes* Nees, ill. Persoon vidit, in ulmo, Chaumont Oise, Octob. 1822", contains sporodochia with a stout stalk, the stalk and the lower part of the head white tomentose, and is form *minor*, attacked by a white Hyphomycete.

T. hysterina Cda., from Corda's figure and description is a small form *minor*, scarcely emergent.

T. marginata Preuss, described from specimens on walnut, is form *minor*, with the conidia washed off the margin, as in *T. ciliata*, judging from the description.

T. pinastri Cda., was based on Libert, *Pl. Crypt. Arduennae* no. 296, on leaves of *Pinus*. The specimens, as previously determined by Paoletti, are form *minor*.

Fries did not include *T. minor* in his list of *Tuberculariа* in *Systema Mycologicum*, though he mentioned it incidentally in his introduction to the genus and in a note under *T. herbarum*. *T. discoidea* and *T. confluens* were also omitted from the list, but, in the Index, Fries gave the former as a synonym of *T. minor* and the latter as a synonym of *T. vulgaris*. Consequently, Fries may be said to have preferred the name, *T. minor*, to the earliest name, *T. discoidea*, but the point is merely of academic interest.

Tuberculariа and *Nectria*

Fries (1823) wrote that the stroma of *Nectria cinnabarina* was very near *Tuberculariа*, "ne dicam idem". Later (1828), he stated that he had satisfied himself that *T. vulgaris* was not an autonomous plant, but an abortive state of *N. cinnabarina*. He also stated (1828), in describing *N. sinopica*, that its stroma was very thin and scarcely evident, but that it was more conspicuous when sterile, when it degenerated into *T. sarmentorum*. The connexion of *N. cinnabarina* with *T. vulgaris* is now accepted, but Fries was mistaken as regards *N. sinopica*.

In *Systema Mycologicum* (1832) Fries wrote, in his introduction to the genus *Tuberculariа*, that species of *Tuberculariа* with a red stratum of conidia closely resembled the stromata of the species of caespitose *Nectria* corresponding to each. Thus, *T. vulgaris* almost always occurred with *N. cinnabarina*, *T. lutescens* with *N. ochracea*, and *T. minor* with *N. coccinea*. As regards the last of these, it must be remembered that Fries's *N. coccinea* evidently covered several species. It has already been noted that *T. lutescens* and *N. ochracea* are merely yellow forms of *T. vulgaris* and *N. cinnabarina* respectively.

Tulasne (1865) fully described *Nectria ditissima* (*N. punicea*) with numerous conidial forms. He stated that the young stromata, the

Tubercularias, were pale rosy, produced only small conidia, and exactly resembled the sporodochia of *T. vulgaris*. But on the bark of elm, they were sometimes mixed with more pallid, *Fusarium* subicula, together with intermediate forms in such abundance that it could not be doubted that they were all the same fungus. The *Fusarium* conidia were cylindric-fusiform, arcuate, obtuse at both ends, subsessile, 5 to 7-septate when mature, up to 60–70 μ long and 5–7 μ broad. Other conidia, more numerous, were ovate or ovate-oblong, continuous, straight, 6–10 × 3·5 μ, apical on rather rigid conidiophores, 30–40 μ long, while others, much less numerous and varying greatly in size, were intermediate between the former two. Before the whole of the conidia had disappeared from the stroma, it became golden and produced numbers of perithecia.

Tulasne stated that the conidial fungus, if he was not mistaken, was sometimes called *Tubercularia minor*. There is little doubt that the rosy sporodochia observed by him were *T. minor*, but his other observations are somewhat puzzling. Fuckel (1869) recorded *Nectria ditissima* on beech, and named the *Tubercularia* which occurred with it *T. crassostipitata*, but he stated that he had not observed the conidia described by Tulasne. I have not seen any *Fusarium* or septate conidium on any of my numerous collections of *T. minor*, on beech, elm, and other hosts, except in one instance, on *Euonymus*, in which a *Fusarium*, which does not agree with Tulasne's description, is parasitic on the *Tubercularia* stromata. This latter *Fusarium* has cylindric, one-septate conidia, 23–27 × 4 μ, apical on simple, septate conidiophores up to 40 μ long. But the *Fusarium* described by Tulasne does occur in cultures originating from ascospores of *Nectria punicea* (*N. ditissima*).

Professor F. T. Brooks has kindly furnished me with a culture obtained from ascospores of *Nectria punicea* on *Rhamnus frangula*, which I identified. The fungus forms white irregular masses, consisting of *Fusarium* conidia, 3 to 6-septate, but often vacuolate and appearing to have more septa, clavate or subcylindrical, straight or slightly curved, ends very obtuse, 36–80 × 6–8 μ. With these are numerous cylindrical or oval, continuous conidia, 9–14 × 4–5 μ, as well as cylindrical, one-septate conidia, about 18 × 5 μ, and wedge-shaped, continuous conidia, 15 × 6 μ. When old, many of the smaller conidia become oval, one-septate, with the cells strongly inflated, and resemble *Nectria* ascospores, 12–16 × 4–6 μ. At the base of the mass, a red parenchymatous stroma is formed, bearing closely-set immature perithecia, or bodies resembling perithecia. Chlamydospores, spherical or oval, are numerous, either terminal or intercalary on the hypha, or occupying the terminal segments of the *Fusarium* conidia. These conidia agree with those figured by Wollenweber (1926) for *N. ditissima*, *N. ditissima* var. *major*, and *N. punicea*, but I have not

observed in the culture anything resembling the conidia and conidiophores of *T. minor*.

Tulasne's observations, at least in part, agree with the results found by cultures from ascospores. It would appear that he observed the earlier stages of development of the stromata of *N. ditissima*, but that he was in error in including as belonging to them the stromata of *T. minor*. There is also the possibility that some of his observations may refer to a Hyphomycete which is commonly parasitic on *Tubercularia*. There is no evident explanation why *T. minor* so often occurs with *N. ditissima* (*N. punicea*).

In the type of *Nectria fuscopurpurea* Wakefield, on *Prunus*, the perithecia are usually smaller than those of *N. cinnabarina*, uniformly encrusted rather than warted, collapsing centrally and becoming pezizoid, and, in addition to normal ascospores of *N. cinnabarina*, have some ascospores two or three-septate, up to $33 \times 8{\cdot}5\,\mu$; these perithecia occur in contact with the sporodochia of *T. minor*. In another collection, on decaying stalks of *Brassica*, in company with *T. minor*, the perithecia are similar, and most of the ascospores are those of *N. cinnabarina*, but some ascospores are cylindrical, two-septate, with the extra septum in one half, $23–27 \times 5–7\mu$. In both examples, *N. fuscopurpurea* is accompanied by *T. minor*.

On the other hand, in a collection on horse-chestnut, the perithecia are warted, but may become cup-shaped on drying, while the ascospores are one-septate, fusoid, $15–30 \times 4–6\mu$, or one-septate, cylindrical, curved, with rounded ends, $30 \times 3\mu$, or one-septate, oblong-oval, from 12×6 to $27 \times 8\mu$, or two-septate, fusoid, $24–30 \times 5–7\mu$, some of the asci being immature, so that it is possible that the longer one-septate spores would have become two or three-septate later; but the accompanying sporodochia are typical *T. vulgaris*. In another collection on elm, the perithecia agree with those of *N. fuscopurpurea*, and the ascospores are one-septate, oblong, fusoid or oval, $12–20 \times 5–8\mu$, with many two-septate, $21–28 \times 6–8\mu$, and some three-septate, $22–30 \times 5–6\mu$; but the accompanying sporodochia are again typical *T. vulgaris*.

In contrast to the foregoing, a collection of typical *N. cinnabarina* on hawthorn and another on *Wistaria* are each accompanied by form *minor*.

Neither the uniform encrustation of the perithecium nor the collapsibility of the perithecia is constant for *N. fuscopurpurea*, and there remains only the occurrence of two or three-septate ascospores. But as most of the ascospores are those of *N. cinnabarina*, it would seem preferable to conclude that the longer, more septate ascospores are an abnormality, which is commoner in *N. cinnabarina* than has been suspected. It is evident from the foregoing records that *N. fuscopurpurea* cannot be separated from *N. cinnabarina* on the ground that it

occurs with *T. minor*, nor can *T. minor* be separated from *T. vulgaris* on the ground of a difference in their perithecial stages.

Wollenweber (1924, 1926) described, as the perithecial stage of *T. minor*, *Nectria cinnabarina* var. *minor*, which occurred with the sporodochia of the *Tubercularia*. The perithecia were gregarious, erumpent, globose, squamulose, red, with a papillate ostiolum, and measured 0·24–0·45 × 0·2–0·42 mm.; the paraphyses were filiform, four- to five-locular; and the ascospores one-septate, oblong, sometimes almost cylindrical, obtuse, straight or slightly curved, generally 12–16 × 4–4·5 μ (10–20 × 3–5·5 μ). He stated that it differed from *N. cinnabarina* in its smaller perithecia, ascospores and conidia. Apparently he did not observe long, two- or three-septate ascospores. It may be queried whether he would have made a new variety, except under the belief that *T. minor* is distinct from *T. vulgaris*.

Tubercularia herbarum Fr.

T. herbarum was described by Fries (1815) as rather large, sessile, subglobose, pale red, internally the same colour, gelatinous when moist, farinose when dry, and occurring on dead herbaceous stems, such as *Cucubalus tartaricus*. Link (1825) included it with Fries's description, giving *T. Artemisiae* Schum. as a synonym. In *Systema Mycologicum* (1832), Fries described it as innato-sessile, with a smooth, pallid (pallido expallente) stratum of conidia, and added that it was quite distinct, minute, pallid, with the habit of *T. persicina* (now *Tuberculina persicina*) but not erumpent. Corda (1829) described it as erumpent, innate, pallid, minute, with a wedge-shaped stroma which was purple internally and covered by a pallid stratum of ovate spores bound together by mucus. Corda's description was adopted by Saccardo (1886).

It seems scarcely possible to harmonize these descriptions. Fries said that *T. herbarum* was rare, and apparently it has not been issued in any exsiccatum. European specimens under this name in British herbaria are obviously misidentified.

Tubercularia versicolor Sacc.

This species was described by Saccardo as having minute sporodochia, sometimes flesh-coloured, sometimes greenish, with conidia apical on filiform conidiophores, ovoid-oblong, 7–9 × 3–3·5 μ, flesh-coloured or greenish, and was figured by him in *Fungi Italici*, pl. 961. It occurred on twigs of box, and Saccardo stated that it was probably the conidial stage of *Nectria Desmazierii*. Neither the description nor the figure conveys much idea of the species, but fortunately Saccardo issued specimens in *Mycotheca Veneta* no. 564.

The sporodochia are circular, pulvinate, up to 1 mm. diameter, or confluent in flat, irregularly oval patches, up to 3 × 2 mm., usually

gregarious, white or pink, dry, not horny or subtranslucent, rather soft. Internally they are white and somewhat loose, with a superficial palisade layer of phialides, which are cylindrical, about 20μ long, 1·5–2μ diameter. The thicker examples are stratose internally, and may have three successive layers of phialides, separated by loosely interwoven hyphae. Thus the sporodochium is "perennial", and as the successive layers are formed before all the conidia of the previous layer have been dispersed, vertical lines of conidia are found embedded in the sporodochium with the old phialides. As noted by Saccardo, some sporodochia may turn green, and that zone of phialides then appears as a dark transverse line in a vertical section of the sporodochium, but the succeeding layers are normally coloured, pink or white. This colour change does not appear to be due to the growth of any other fungus, though conidia of *Penicillium* have been observed in a discoloured layer; a similar colour change occurs in the conidial masses of some species of *Aschersonia*. The conidia are hyaline, subcylindrical or oval, 4–9 × 2–3μ, sometimes subglobose, 3μ diameter. The base may be oblique in the subcylindrical conidia, and sometimes broadly apiculate in the oval conidia. They are produced in chains at the apices of the phialides.

At the margin of the sporodochium, it is sometimes possible to find free conidiophores which show how the loose stroma is built up. These conidiophores have a main stem, 2μ diameter, rather closely septate above, with a short branch from each node, each branch bearing one or a cluster of three phialides, which all attain the same level. The loose tissue beneath is formed by the interlacing and fusion of the branches, while the phialides form a continuous superficial layer. The branching is similar to that of a *Spicaria* or *Gliocladium*.

Paoletti stated that the conidiophores were septate, and separated readily into cylindrical joints. From his figure, it would appear that what he took for the stalks of the conidiophores were the chains of conidia embedded in the sporodochium.

Tubercularia versicolor was recorded as occurring in this country in Massee's *British Fungus Flora*, but I did not find any British specimens at Kew or the British Museum. It is, however, not uncommon, and frequently occurs in company with various species of *Nectria*. I have collections of it with *N. sinopica* on ivy, with *N. punicea* on broom, with *N. mammoidea* on sycamore, and with *N. coccinea* on elm. It may be that this species prefers bark which has been attacked by a *Nectria*, or that it prefers fungi in general, as I have another collection on the stalk of *Polyporus squamosus*.

A similar fungus was collected by Libert on decaying stalks of *Brassica*, and was issued in *Libert* no. suppl. 634 as *Dendrodochium rubellum* var. *Brassicae*. It forms minute, white or pink, pulvinate or subglobose sporodochia, about 0·5 mm. diameter, which become

confluent in small, flat patches and turn fawn-coloured when old. The sporodochia are usually closely gregarious and may cover a length of several inches. Internally they are loose, but in the larger examples are rather more compact than in *T. versicolor*, with a deeper conidiiferous layer. The latter appears in section to have septate phialides, but actually it has septate conidiophores, with lateral branches like those of *T. versicolor*, each branch terminating in a small cluster of phialides. The septa are those of the conidiophore, the phialides being shorter than those of *T. versicolor*, but of the same shape, cylindrical, 12 μ long, 2 μ diameter. In this species the conidiophores are fused at their bases, so that it has free, branched conidiophores and is probably correctly placed in *Dendrodochium*, though the type of branching is spicarioid, and not that usually associated with *Dendrodochium*. The conidia are hyaline, cylindrical or oblong-oval, 5–7 × 2–3 μ, sometimes subglobose, 4 μ diameter. I have not observed conidia in chains, nor have I found stratose sporodochia.

Dendrodochium rubellum var. *Brassicae* does not appear to have been recorded for this country, though it is quite common on decaying stalks of *Brassica*. It is, however, to be found in the herbaria of Kew and the British Museum, where it constitutes the chief part of the fungi now remaining on the type specimens of *Nectria Keithii* B. & Br., and *Nectria furfurella* B. & Br., both of which are on decaying stalks of *Brassica*.

Tubercularia nigricans (Bull.) Gmel.

This species was described and figured by Bulliard (1784) as *Tremella nigricans*, and was transferred to *Tubercularia* by Gmelin (1791), with the brief description, "at first red, then black". De Candolle (1805) stated that it greatly resembled *T. vulgaris*, but the sporodochia were larger and not contracted at the base, at first bright red, becoming covered with a white film and turning black when old, details taken or deduced from Bulliard's description and figures.

Link (1825) included it in his list of *Tubercularia*, and described it as rather large, immersed, red, arising from flocci, with a stratum of conidia of the same colour, the sporodochium and the stratum of conidia at length black. Link appears to have thought that the fungus first appeared as a patch of white hyphae, on which the stroma developed, as he described for *T. floccipes*, probably a misinterpretation of the white zone on the sporodochia in Bulliard's figures. Fries included it in *Systema Mycologicum* (1832) as *T. nigricans* DC., stating that it scarcely differed from *T. vulgaris*.

Sporodochia of *T. vulgaris* may blacken for various reasons, but the black examples are not always *T. nigricans*. I have, however, recently collected specimens which correspond with Bulliard's figures, though I have not seen any sporodochia which are covered by a white

film, other than those, commonly found, covered by white parasitic Hyphomycetes, which do not turn black. Bulliard's figures show rather flat sporodochia, some red, others black, others partly red and partly black, with a narrow, white, byssoid zone, surrounding the red area, which may be lateral or central. The peculiarity of these figures is the sharp contrast between the peripheral black zone and the normally red area of *T. vulgaris*.

The recent specimens occurred at North Wootton, on horse-chestnut and on elm, and at Steeton, Tadcaster, on sycamore, coll. W. G. Bramley, all in company with *T. vulgaris*. These show that *T. nigricans* is wholly or partially parasitized *T. vulgaris*. The totally black sporodochia, when viewed in section macroscopically, are dirty reddish below, with a black peripheral zone. In thin sections, by transmitted light, this peripheral zone is fuscous below, almost hyaline above, with an irregular black line at the outer edge. It consists of a basal zone of large-celled parenchyma, from which arise crowded, parallel conidiophores. These conidiophores are up to 150μ long, 1·5–2μ diameter, once or twice forked, regular, fuscous at the base, greenish hyaline above, and pass above into chains of cylindrical, truncate, greenish hyaline conidia, $6-12 \times 1{\cdot}5-2\mu$. Stout, fuscous, irregular hyphae, 4μ diameter, run from the basal stroma, or from the base of the original *T. vulgaris* stroma, through the layer of conidiophores, often in coarse fascicles, and may terminate in conidiophores, or may spread out over the surface of the sporodochium in a single discontinuous layer. The colour of the sporodochium, however, appears to be due principally to that of the stratum of conidiophores. Very little of the original *Tubercularia* stroma may remain unaltered in these black sporodochia, and what there is may be permeated by fuscous hyphae.

In the sporodochia which bear a red patch, surrounded by a black zone, the structure of the black region is the same as that described above. But the red area consists of normal conidiophores and conidia of *T. vulgaris*, arising from normal stromatic tissue of that fungus and passing in a column through the conidial layer of the parasite.

The statement that the sporodochium of *T. nigricans* is at first red and finally black was no doubt a deduction from the fact that red, black, and partly red and partly black sporodochia occur together. But no conidiophores of *T. vulgaris* have been found beneath the black areas, and there is no evidence that the parasite grows gradually over the fully-developed sporodochia of *T. vulgaris*. From examination of these recent specimens it would appear that the sporodochium of the latter is attacked at an early stage. Some escape attack and are consequently red, others are completely attacked and are black, developing only the conidiophores of the parasite, while others have been only partly attacked and so have developed in part normally.

Whether the white fringe surrounding the red area in Bulliard's figures belongs to the parasite or to its host cannot be decided from the available specimens.

Nees sent a specimen to Link, named *T. mutabilis*, and it was published by Link (1825) under that name. According to the description it was at first red, then black, and Link stated that when young it was indistinguishable from *T. vulgaris*, but when old it became almost completely black, and that the change seemed to occur suddenly, unless it was that black and red examples occurred together from the beginning; it differed from *T. nigricans* in the absence of flocci. Link, however, was mistaken in believing that *T. nigricans* arose from a floccose stratum, and it seems most probable that *T. mutabilis* was *T. nigricans*. The only herbarium specimens I have found under the former name are *West. Herb. Crypt. Belg.* no. 1191 on *Kerria*; these in the specimen examined are simply *T. vulgaris*, and do not agree with Link's description.

Tulasne (1865) figured the conidiophore and conidia of this parasite of *T. vulgaris* as the conidial stage of *Nitschkea cupularis*, stating that the conidiophores broke up into truncate conidia, not more than 10 μ long. He described the affected stromata of *Nectria cinnabarina* as variegated with black, both inside and out, and sometimes wholly black, but it is uncertain how much of this was due to *Nitschkea* and how much to the parasite described above. There is no other record of such a conidial stage of *N. cupularis*, and the latter does not occur on my recent specimens. It has not been determined what the parasite which converts *T. vulgaris* into *T. nigricans* is, though it scarcely seems probable that it has not been described under some name or other. Apparently it should not be classed as a Hyphomycete, as it has a superficial layer of hyphae over the conidiophores. It does not agree with the description of *Cylindrocolla episphaeria* v. Höhnel, the spores of which were said to be 14–26 × 3–3·5 μ.

Tubercularia granulata Pers.

This species was described by Persoon (1801) as subrotund, sordid red, surface rugoso-tuberculate. He added that it became sordid fuscous in colour, and was opaque, yellowish ochraceous internally, the surface undulato-rugose and rough here and there with unequal granules. It occurred rather rarely on branches of *Acer platanoides* and *A. pseudo-platanus*.

Fries (1815) described *T. liceoides* Fr. as gregarious, sessile, globose, with a fuscous, rufous brown, deciduous cortex, and an "argillaceo-rosea" powder covering the nucleus (stroma). He added that it was often confluent, smooth, granuliform, with granules the size of seeds of *Vicia*, rarely of *Pisum*; the cortex was rufo-fuscous or fuscous brown, ultimately deciduous, when a subcompact, copious, "argillaceo-

rosea" powder covered the stroma, which was rather hard and pallid internally, surrounded by a darker fuscous zone. It will be noted that the "granules" in Fries's description mean the whole sporodochia, while in Persoon's they are roughnesses on the surface of the individual sporodochium.

Link (1825) included *T. granulata* with the description, sporodochia immersed, white, stratum of conidia convex, sordid red, finally blackening; and *T. liceoides* with Fries's description, except that he altered "argillaceo-rosea" to "argillaceo-fusca".

In *Systema Mycologicum* (1832), Fries included *T. granulata* Pers. with the description, stratum of conidia rugose, sordid red, finally fuscous, margin naked, and added that it was always sordid and finally blackening, ultimately granuliform and compact, and then the outer hard stratum was loosened and the interior became powdery, in which last state it was *T. liceoides* Fr. Thus Fries withdrew *T. liceoides* as a synonym of *T. granulata*, but he does appear to have been quite decided about it, as in a later list (1849) he included *T. liceoides* as a species near *T. granulata*.

Wallroth (1833) gave a description of *T. granulata* which states that the sporodochium emits conidia in drops of liquid which do not flow over the surface, but harden like drops of gum, a statement which sounds fantastic, but one which might be true under some conditions.

The principal characters of *T. granulata*, according to the foregoing descriptions, are the granular surface of the sporodochium and its ultimate blackening. As regards the first, normal specimens of *T. vulgaris* often have an irregular or granular surface, so that this character does not separate *T. granulata* from the latter species. There remains, therefore, only the blackening of the sporodochium, which from Fries's account was a superficial blackening.

Discoloured sporodochia of *T. vulgaris* are quite common. They occur with normally coloured sporodochia, and may be sordid red, brownish red, brown or black, but the black specimens usually appear brown or dull orange when soaked in water. In general, the brown or black colour is confined to a superficial film, underneath which are normal conidiophores and conidia of *T. vulgaris*. The film binds together conidia and the tips of the conidiophores, and in herbarium specimens the embedded conidia may be brown. There is no general covering of foreign mycelium, but sometimes a few blackish or fuscous cells, cuboid, 4–5 μ diameter, or oval, up to $9 \times 6 \mu$, in short, irregular chains at the ends of fuscous hyphae, 2 μ diameter, may be found. These are *Torula Tuberculariae* Nees. Brown or black amorphous bodies, and black stromatic bodies, oval, $34 \times 27 \mu$, or globose, about 50 μ diameter, sometimes occur, but neither these nor the chains of cells are ever sufficient to account for the general blackening, and they may be quite absent. In addition, one finds algal cells and

miscellaneous fungus spores on some specimens. The superficial film is insoluble in water, and it would appear that the mucus which normally involves the conidia has become changed at the surface of the sporodochium. The cause of this modification has not been ascertained. Ultimately the hard outer layer may break away, exposing the interior mass of conidiophores and conidia, in which state the fungus is *T. liceoides* Fr.

T. granulata, in Fries *Sclerom. Suec.* no. 257, agrees with the foregoing description. In Herb. British Museum, there is a specimen of *T. liceoides*, *ex* Herb. Shuttleworth, marked by Schmidt, "ab ipso", i.e. from Fries. It contains small, brown, regular, pulvinate sporodochia, which are *T. granulata*, and others pallid to brownish, with an irregular surface, the upper part of the sporodochium having broken away. A specimen from Greville, from woods in Durham, in Herb. Kew., determined as *T. liceoides*, is *T. granulata*, and does not differ from another Durham specimen from Greville, determined as the latter species.

Paoletti took as his example of *T. granulata*, a specimen in Saccardo *Mycoth. Venet.* no. 565, issued as *T. granulata f. Robiniae Pseudacaciae*. From his description, his specimen was a plain, stalked form *minor*, and an examination of the exsiccatum cited confirmed that. It does not show the colours or the superficial film of *T. granulata*.

Corda (1838) described a variety *cava* of *T. granulata*. His figure of the vertical section shows a narrow transverse fissure near the upper surface of the sporodochium, and below that another, independent, laterally oval cavity. The transverse fissure is probably the initial stage of the scaling off. The lower oval cavity does not resemble that found in form *minor*, and it looks rather like the work of an insect. Von Thümen issued specimens on *Populus* in *Fungi Austriaci* as *T. cava*, but these are not hollow and are merely *T. granulata*. He also recorded *T. cava* from Siberia (1880), and stated that some of the conidia were almost subclavate, which makes it probable that he had form *minor*. In the latter instance, he described the conidia as cylindrical, ends rounded, $4–6 \times 2–5 \mu$, and that measurement is quoted by Saccardo (1886), but it seems probable that the breadth given is a printer's error for 2·5.

Von Thümen also described a new species, *T. Berberidis*, and issued specimens of it in *Mycoth. Univ.* no. 696. The sporodochia in the Kew copy of this resemble a Discomycete. They have a well-developed, immersed stalk, and a concave, or plane, or slightly convex, reddish disk, with a brown, rounded margin, sometimes separated from the reddish disk by a circumferential furrow. Examination shows that the disk is composed of the conidiophores and conidia of *T. vulgaris*, while the brown margin has the surface structure of *T. granulata*. They are specimens of *T. granulata*, from the centre of which the continuous

outer layer has scaled off, as described by Fries for his *T. liceoides*. There is a similar specimen in Herb. Kew., marked by Berkeley, "*Sphaeria Berberidis* praecursor, Wansford, Norths., *ex* Herb. Berk.", and placed subsequently in the cover of *T. Berberidis*.

British species of *Tubercularia*

In 1836, Berkeley recorded for Britain *T. vulgaris* Tode, *T. granulata* Pers., and *T. nigricans* Link. He stated that the last-named was probably only a variety of *T. vulgaris*; that *T. discoidea* and *T. confluens* were forms of *T. vulgaris*; and that *T. minor* differed only in size, and was common on *Robinia Pseudacacia*. No further species were added by Berkeley and Broome in their *Notices of British Fungi*. In 1893, Massee enumerated seventeen British species, which are dealt with below, together with others, named in herbaria but apparently unrecorded as British.

T. vulgaris Tode. Common. The numerous herbarium specimens under this name have not been examined.

T. minor Link. A form of *T. vulgaris*. Common. Baxter no. 100 (as *T. discoidea*); on cherry laurel, Kew (Cooke), Herb. Kew. *T. minor* var. *Syringae* Cke. and Massee is ordinary form *minor*. Sowerby's figure of *Clavaria coccinea*, pl. 294, appears to be form *minor*.

T. granulata Pers. Modified *T. vulgaris*. Common. Numerous British specimens in Herb. Kew., including one from Durham (Greville), and another from Glamis (Herb. Berk.).

T. liceoides Fr. Dehisced *T. granulata*. A specimen in Herb. Kew. under this name, from woods in Durham (Greville), is *T. granulata*.

T. nigricans (Bull.) Gmel. Parasitized *T. vulgaris*. Recorded by Berkeley from King's Cliffe, Norths., but his specimen is not available. British specimens under this name are usually *T. granulata*, e.g. Vize, *Microfungi Britt.* no. 353, from Forden; specimen in Herb. B.M. from Bloxam without date or locality; Thirsk (J. G. Baker), Herb. Kew.; Bungay (Stock), with normal *T. vulgaris*, Herb. Kew. I have recent specimens of *T. nigricans* on elm and horse-chestnut from North Wootton, and on sycamore, Steeton, Yorks. (W. G. Bramley).

T. Aesculi Opiz. Specimen, Kew, October 1887 (Cooke), in Herb. Kew., is *T. vulgaris*.

T. Sambuci Cda. Rhodes 3313 is *T. vulgaris*. Specimen, Roehampton, 20 March 1887 (E. G. Baker), in Herb. Kew., is *T. vulgaris*. Kew, 18 April 1885 (Cooke), in Herb. Kew., is a *Fusarium*.

T. aquifolia Cke. & Massee. The type specimen is *T. vulgaris*.

T. conorum Cke. & Massee. The type is *T. vulgaris*.

T. sarmentorum Fr. The only British specimen under this name, on *Ptelea trifoliata*, Kew. (Massee), Herb. Kew., is *T. vulgaris* form *minor*.

T. subpedicellata Schw. The only British specimen, on lilac, Kew (Cooke), is *T. vulgaris* form *minor*. A North American specimen from Schweinitz in Herb. Kew. is now unserviceable.

T. Euonymi Roum. The only British specimen, Kew Gardens, September 1887, is *T. vulgaris* form *minor*.

T. herbarum Fr. British specimens under this name are misnamed. Specimen on *Dulcamara*, Kew, 1885 (Cooke), Herb. Kew., is *T. vulgaris* form *minor*. Another on *Anthriscus*, Honington, Suffolk (Cooke), Herb. Kew., is *Dendrodochium rubellum* var. *Brassicae* Libert.

T. Brassicae Libert. British specimens are *T. vulgaris* form *minor*.

T. Berberidis Thum. A British specimen in Herb. Kew., *ex* Herb. Berk., Wansford, is *T. granulata*, i.e. modified *T. vulgaris*.

T. floccosa Link. A specimen in Herb. Kew. under this name, on *Rhus radicans*, Kew (Cooke), is *T. vulgaris* becoming *T. granulata* and attacked by *Torula Tuberculariae* Nees.

T. expallens Fr. A specimen under this name in Herb. Kew., Kew Gardens, October 1887 (Cooke), is too immature for identification, but certainly not *T. expallens* and probably not *Tubercularia*.

T. Ligustri Cooke. There are several fungi in Cooke's type, but the one described, and figured by him in Herb. Kew., is *Dendrophoma pleurospora* Sacc.

T. versicolor Sacc. No British specimens, though it is not uncommon in this country. I have recent specimens from Norwich, North Wootton, Becca Park (Yorks.), Kinlet, and Dartington.

Thus the only species of *Tubercularia* known to occur in Britain are *T. vulgaris* and *T. versicolor*.

Fungi parasitic on *Tubercularia* and *Nectria*

In the host index to Saccardo, *Sylloge Fungorum* (vol. xiii), the following fungi are recorded as parasitic on *Tubercularia*—*Cladosporium penicillioides* Preuss, *Coniothyrium Tuberculariae* Pass., *Graphium pelitnopus* (Cda.) Sacc., *Oedocephalum glomerulosum* (Bull.) Sacc., *Sphaeria parasitans* Schw., *Torula Tuberculariae* Nees, and *Verticillium epimyces* B. & Br. The last-named was probably included in error, as this species was described from specimens on *Elaphomyces* (Tuberoideae). In the same volume, *Hormiactis Nectriae* Karst., is given on *N. coccinea*, and *Oospora nectriicola* Rich., on *N. Dahliae*. Grove (1885) recorded *Oospora candidula* Sacc., on *N. cinnabarina* in England, and Hennings described *Fusarium Nectriae-Turriae* P. Henn., on *N. Turriae* from Africa. Von Höhnel (1904) recorded *Oospora hyalinula* Sacc., on *N. Peziza*, and published (1917) the names of two new species, *Pedilospora episphaeria* and *Cylindrocolla episphaeria* on effete *N. cucurbitula*; his description of the latter was published by Weese (1924), but the former is apparently *nomen nudum*.

Oospora sp. indet.

This species occurred in abundance on *T. vulgaris* (including form *minor*) at North Wootton. It forms a compact, white or cream-coloured crust which ultimately covers the whole sporodochium and spreads out in a strigose patch over the bark. The basal hyphae are up to 6 μ diameter. The conidiophores and conidia are very variable in size. In some specimens, the conidiophores are up to 100 μ high, 5–6 μ diameter at the base, attenuated upwards to 2 μ diameter at the truncate apex, sometimes curved at the base, simple or with one lateral branch, septate, hyaline, while the conidia are oblong-oval, with a broad, truncate apiculus, hyaline, smooth, 10–18 × 4–6 μ. In others, the conidiophores are the same shape, but about 40 μ high, 3 μ diameter below, tapering to 1 μ at the apex, and the conidia oblong-oval, oval, or narrow-oval, sometimes fusoid, ends rounded, rarely with a truncate apiculus, 5–9 × 1·5–2·5 μ. Both forms may occur on the same sporodochium, but, in general, the smaller form is the more common and may be the only one present.

If a sporodochium on which the white crust is just beginning to develop, or a sporodochium from an infected group which does not bear any external sign of the parasite, is wetted and placed in a damp chamber, it usually produces, within twenty-four hours, long, scattered, hair-like conidiophores of the larger kind, with large conidia in long chains. But if it is left and allowed to become drier, these conidiophores are followed by the development of the continuous white crust and smaller conidiophores. Under natural conditions, chains of conidia are rarely seen, a cluster of three or four conidia adhering to the apex of the conidiophore. I have not been able to identify this species, and as it seems incredible that it should not have been described or recorded, it would appear best to leave it anonymous for the present.

As indicated above, sporodochia which are apparently unattacked may occur on a branch in close proximity to others which bear the white crust. The former, however, are usually infected, though the parasite has not developed far enough to be evident externally. They are usually deep red internally, and when a section is mounted in water, it exudes numbers of hyaline or reddish oil globules. The conidiophores do not separate readily from one another, as they do in normal *T. vulgaris*. Irregularly flexuose, hyaline hyphae, 1 μ diameter, run transversely through the zone of *Tubercularia* conidiophores. Some of the conidiophores are normal in structure, 2 μ diameter, but their contents are granular. Others are stouter, 3 μ diameter, branched, with their contents aggregated into oily, irregularly cylindrical or oblong-oval masses, up to 9 μ long. Long lengths of these stouter conidiophores lack conidia, but here and there one finds on

them the short lateral branches and apical conidia of *T. vulgaris*. It would appear that these abnormalities are due to the attack of the *Oospora* on the *Tubercularia* sporodochia. Such sporodochia appear to be most common in the early months of the year; I had great difficulty in finding normal sporodochia in my stick-heaps (apple, birch, etc.) in February.

The *Oospora* described above does not appear to agree with the brief description of *O. nectriicola* Richon. Richon (1889) named his species twice, first *O. nectriaecola* and again as *O. Sphaerella*. It occurred on *Nectria Dahliae* Richon, apparently a *Dialonectria*, of which he considered it the conidial stage. Some perithecia were covered with white tufts of short conidiophores, once or twice septate, which bore ovoid, hyaline conidia, at first in chains, then scattered. Dimensions were not given, and the details available are insufficient for determination. The species on *Tubercularia* described above forms a continuous crust, not tufts. Lindau, in *Rabh. Krypt. Flora*, VIII, 30 (date of part, May 1904) credited von Höhnel with the discovery of *O. nectriicola* on *N. Magnusiana*, but later in the same year von Höhnel (1904) stated that it was an insufficiently described species.

Oospora candidula Sacc., etc.

O. candidula was described and figured by Saccardo (1878) from specimens on leaves of *Acer*. At the same time, he referred to it a fungus found on decaying woody fungi, which he had previously assigned to *Torula candida* (Wallr.) Opiz in *Mycol. Venetae Specimen* (1873), 177. Saccardo's figure of the fungus on *Acer* shows short, equal conidiophores, not inflated at the base, bearing long chains of oval conidia, $5–6 \times 3\mu$.

O. candidula was recorded for England, on *Tubercularia vulgaris*, *Nectria cinnabarina*, and the adjacent bark, by Grove (1885), who repeated Saccardo's description. Through the kindness of Dr C. G. C. Chesters, I have been able to examine Grove's specimen. The *Oospora* forms small, white, floccose tufts, which bear short columns of conidia here and there. The conidiophores are short, equal or conoid, sometimes fusoid, about 25μ high, 4μ diameter below, 3μ diameter above, each bearing an apical chain of conidia, broader than the conidiophore. The conidia are cuboid or cylindrical, or slightly barrel-shaped, sometimes broader than long, the smaller becoming subglobose, $3–6 \times 4–5\mu$. The chains of conidia from adjacent conidiophores sometimes adhere laterally. This is an *Oospora*, and it may be left under Saccardo's name, though the recorded range of hosts appears open to question.

Von Höhnel (1904) recorded another species, *O. hyalinula* Sacc., on *Nectria Peziza*, giving the conidia as oblong, straight, $5–7 \times 2–2{\cdot}5\mu$ (Saccardo gave the dimensions, $4–6 \times 1{\cdot}5–2\mu$). He added that *O.*

candidula Sacc., was very similar, but had broader conidia (probably judging from the descriptions), and that *O. nectriicola* Rich., was insufficiently described, but probably identical with *O. hyalinula*. The last-named was originally described as parasitic on *Capnodium Footii* on Olive.

In August 1935, I collected a Hyphomycete at Helmsley, Yorks., on *Nectria coccinea* and the surrounding sycamore bark. The fungus forms small, loose, white tufts, bristling with columns of conidia. The basal hyphae are stout, septate, 4μ diameter, interwoven into a loose stroma, or running separately over the host. The conidiophores are rigid, erect, clustered, hyaline, or slightly fuscous at the base, white in mass, up to 50μ high, 4μ diameter and ovoid or conoid at the base, attenuated into a long, cylindrical tube, 2μ diameter, not septate, producing a persistent chain of cylindrical, truncate, hyaline conidia, 3–6 × 2μ. The chains of conidia are often laterally adherent in columns, which appear as a series of bristles. This appears to be a *Chalara*, and I recorded it as *Chalara fusidioides* Cda., but it would seem probable that it is the fungus recorded by von Höhnel as *Oospora hyalinula*.

Torula Tuberculariae Nees

This species was figured by Corda (1829, pl. 47) as forming minute black spots or streaks on the sporodochia of *T. vulgaris*. Link (1824) founded for it a new genus, *Tetracolium*, but that has not been accepted. *Tetracolium* was defined as having decumbent, adpressed hyphae, with conidia in chains of four, but, as is shown in Corda's figure, there may be more than four "conidia" in a chain. The best examples I have seen of this species were on a specimen of *T. vulgaris* on *Rhus radicans*, collected at Kew and assigned by Cooke to *T. floccosa*. The mycelium is hyaline to fuscous, coarse and irregular, 2–4μ diameter, repent, terminating in adpressed chains or clusters of blackish cells, cuboid, 4–12μ broad, or ovoid, up to 9 × 6μ. This species does not appear to occur in sufficient quantity to cause a general blackening of the sporodochium.

Some synonyms of *Tuberculariа vulgaris*

T. Aesculi Opiz, in Corda, *Ic. Fung.*, I (1837), 4.
T. Ailanthi Cke., in *Grevillea*, XII (1883), 26.
T. aquifolia Cke. & Massee, in *Grevillea*, XVI (1887), 49.
T. Artemisiae Schum., *Enum. Plant. Saell.*, II (1803), 183.
T. conorum Cke. & Massee, in *Grevillea*, XVI (1887), 49.
T. lutescens Link, *Sp. Plant.*, VI, 2 (1825), 100.
T. Menispermi Fr., *Obs. Mycol.*, I (1815), 208.
T. Populi Schum., *Enum. Plant. Saell.*, II (1803), 184.
T. Pruni Schum., *Enum. Plant. Saell.*, II (1803), 183.

T. Rhamni Paol., in *Atti Soc. Ven. Trent.*, XI (1887), 59.
T. Ribesii Westend. (as var. *Ribesii*), *Les Cryptogames classes*, etc. (1854), 119.
T. Robiniae Kickx, *Fl. Crypt. Flandres*, II (1867), 106.
T. Sambuci Cda., *Ic. Fung.*, I (1837), 4.
T. sarmentorum Fr., *Obs. Mycol.*, I (1815), 208.

Form *minor* Link

T. Acaciae Fr., *Obs. Mycol.*, I (1815), 207.
T. Brassicae Lib., Herb. no. 1019; Saccardo, *Mich.* II (1882), 644.
T. Castaneae Pers., *Synopsis* (1801), 114.
T. ciliata Ditm., *Sturm's Deutschl. Fl.*, III, I (1817), 29.
T. confluens Pers., *Synopsis* (1801), 113.
T. Coryli Paol., *Atti Soc. Ven. Trent.*, XI (1887), 59.
T. crassostipitata Fuck., *Symb. Mycol.* (1869), 180.
T. discoidea Pers., *Obs. Mycol.*, I (1796), 79.
T. Euonymi Roum., *Fung. Sel. Gall. Exsicc.* no. 55.
T. expallens Fr., *Syst. Mycol.*, Index, 197.
T. floccipes Cda., in *Sturm's Deutschl. Fl.*, III, 2 (1829), 53.
T. floccosa Link, Obs., etc., Diss. secunda. *Mag. d. Ges. nat. Freunde, Berlin*, VII (1816), 32.
T. hysterina Cda., *Ic. Fung.*, I (1837), 4.
T. longipes Peyl, in *Lotos*, VII (1857), 66.
T. marginata Preuss, *Fung. Hoyersw.* no. 163.
T. minor Link, *Sp. Plant.*, VI, 2 (1825), 100.
T. pinastri Cda., *Ic. Fung.*, III (1839), 33.
T. vaginata Cda., *Ic. Fung.*, I (1837), 4.
T. velutipes Nees, *System d. Pilze*, etc. (1817), 35.

Modified *T. vulgaris* (*T. granulata*)

T. Berberidis Thüm., *Mycoth. Univ.* no. 696.
T. cava Thüm., in *Bull. Soc. Impér. d. Naturalistes*, LV (1880), 203.
T. granulata Pers., *Synopsis* (1801), 113.
T. granulata var. *cava* Cda., *Ic. Fung.*, II (1838), 33.
T. liceoides Fr., *Obs. Mycol.*, I (1815), 208.

Parasitized *T. vulgaris*

T. mutabilis Nees, in Link, *Sp. Plant.*, VI, 2 (1825), 101.
T. nigricans (Bull.) Gmel., *Syst. Nat.*, ed. XIII, II, 2 (1791), 1482.

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NEW AND INTERESTING PLANT DISEASES

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(With Plate III)

4. Septoria leaf blotch of *Lobelia*

In August 1939 Mr W. Buddin sent me a badly diseased plant of *Lobelia syphilitica* var. *nana* obtained from a nursery near Maidenhead. Individual leaves exhibited irregular pallid spots or blotches, spreading inwards from the margins or tips, and bordered by rather broad, indefinite, pink or mauve-pink bands (Pl. III, fig. 1). Many of the older leaves had been killed by the disease and only the youngest foliage was unaffected. Numerous black pycnidia of a *Septoria* were present in small groups scattered over the upper, and occasionally the under surface of the affected leaves. They were 75–150 μ in diameter, with a clearly defined ostiole, and contained thread-like, hyaline spores, straight or slightly curved, with rounded ends, indistinctly septate, measuring 18–30 × 1–1·5 μ (average length 23 μ).

In the literature, species of *Septoria* have been recorded on *Lobelia* in North America and Germany. *Septoria Lobeliae* Peck was described from New York State by Peck (1874) on *Lobelia spicata*, the leaves of which exhibited pallid spots, round or often confluent, with black or purple-brown margins. The pycnidia were stated to be minute, numerous, black, adpressed, with simple filiform spores 17–25 μ long. The same species has also been listed from North America on *L. cardinalis*, *L. inflata* and *L. syphilitica*. According to Martin (1887) the pycnidia occur in clusters and are 100–130 μ in diameter, with spores measuring 26–40 × 1–1·5 μ, while Uppal (1925) cited the spore measurements as 14–34 (mostly 20–28) × about 2 μ. Two varieties of this species have been described. The pycnidia of *Septoria Lobeliae* Peck var. *berolinensis* Syd. (1899), on *Lobelia inflata* in Germany, are 80 μ in diameter, with unicellular spores 20–26 × 1·5 μ, and var. *Lobeliae-inflatae* Sacc. (1915), on the same host in North America, is said to differ from the type by the somewhat larger spores (28–30 × 1·8 μ). Both these varieties, however, agree substantially with the American conception of *Septoria Lobeliae* Peck. On the other hand, *S. Lobeliae-syphiliticae* P. Henn. (1895), on *Lobelia syphilitica* in Germany, with spores 44–55 × 1–1·5 μ, and *Septoria ramonensis* Syd. (1926), on *Lobelia laxiflora* in Costa Rica, with spore measurements of 27–55 × 2–2·5 μ, are evidently distinct.

Type material of these fungi was not available for examination, but there are three specimens in the Kew Herbarium which are referred to *Septoria Lobeliae* Peck. One of these is labelled "on *Lobelia*, first European record 24/2/10", and Miss E. M. Wakefield has kindly informed me that it had been collected at Geashill, King's Co., Ireland, and was identified by Massee. The host appears to be a form of *L. erinus* and the fungus agrees very well with my own material and with the description of *Septoria Lobeliae* Peck. The second specimen, distributed in Ell. & Ev. *N. Amer. Fungi*, 2nd ser. no. 1732 on *Lobelia inflata* from Massachusetts, appears to be the same fungus, though its spores on the whole are longer (24–39 μ with an average of 30 μ), and many of them are distinctly septate. The other specimen, collected in Costa Rica by F. L. Stevens, is a different species corresponding closely to the description of *Septoria ramonensis* Syd.

5. *Septoria* sp. and *Ascochyta bohemica* on *Campanula*

Specimens of *Campanula* grown on the same nursery as the *Lobelia* mentioned above, and examined at the same time, were affected by two distinct diseases. The foliage of *Campanula Raineri* showed irregular brown blotches, bounded at first by the veins, but later spreading over the leaves and killing them. Pycnidia of a species of *Septoria*, distinct from the one on the allied host *Lobelia*, were present in large numbers on the affected areas. They were scattered or aggregated, amphigenous, black, 60–105 μ in diameter, with a well-defined ostiole up to 24 μ across. The spores were more variable, longer and distinctly broader than those of *S. Lobeliae*, straight, or more often slightly or markedly curved, hyaline, aseptate or distinctly 1–3 septate, with rounded ends, 17–38 × 1·5–3 μ (average length of 50 spores 27 μ).

Septoria obscura Trail was recorded on living leaves of *Campanula rotundifolia* in Britain in 1889. Its pycnidia occur on round or irregular, dingy brown spots having narrow and indistinct dark borders, and are amphigenous, scattered, immersed, black and with short ostioles. The spores are cylindric-filiform, obtuse at the ends, curved, 3-septate, yellowish and measure 22–35 × 1·5 μ. I have not examined material of this species but the fungus collected at Maidenhead does not appear to differ from the description of it except in the width and colour of the spores.

Ascochyta bohemica Kab. & Bub. was found on dead portions of the stems, petioles, leaves, calyces and withered petals of living plants of *Campanula betulaefolia*, as well as on the foliage of *C. Raineri*. The pycnidia were 90–180 μ in diameter, scattered, immersed, indefinite, and pale brown, but darker or almost black around the clearly defined ostiole. The spores, which issued in tendrils, measured 12–21 × 4–6 μ (mostly 18–19 μ long) and were hyaline, continuous or one

septate, straight or slightly constricted at the septum, with one or more oil drops in each cell. The spores resembled those of *Stagonospora* except that none was found with more than one transverse wall.

Ascochyta bohemica was described on *Campanula Trachelium* in Bohemia in 1905, and has not previously been recorded in this country. Two Latvian specimens on *C. Trachelium* (ex. J. Smarods Herb.) in the Kew Herbarium have been examined. Both showed local hypertrophied spots on the veins, with only a few pycnidia. The spores in this material were rarely longer than 16μ or broader than 4μ.

6. Root and bulb rot of tulips caused by *Pythium*

A *Pythium* disease of forced tulips has occasionally been observed in recent years in England and on the Continent (Moore, 1939, p. 33). It is primarily a root trouble, but in the later stages of attack the bulbs of some varieties may also be affected. The disease was described and the first English records enumerated by Moore & Buddin (1937), and it has been observed since under glass in the varieties Prof. Rauwenhof (Hants, 1938), Allard Pierson (Lincs, 1938) and William Copland (Middlesex, 1939). Other specimens, examined at the end of November 1938, revealed that the disease may develop before the tulips are housed, and demonstrated the important bearing of high soil moisture on its appearance and severity. On a large nursery in Essex about 60,000 boxes of various commercial varieties of tulips, planted in unsterilized soil, had been plunged in a mixture of soil and ashes out of doors, preparatory to forcing. Heavy rain had fallen during October and November, and the bottom inch or two of soil in the boxes was practically waterlogged. Many of the plants in representative boxes of William Copland, William Pitt and Allard Pierson showed typical symptoms of *Pythium* root rot, and *Pythium* was isolated from the brown, decayed distal portions of affected roots. Although the bulbs and much of the older portions of the roots were still sound, severe losses during forcing appeared to be almost inevitable. Nevertheless, by taking the boxes indoors as soon as possible, allowing them to drain off on the staging, and subsequently reducing watering to a minimum, the disease was quickly checked, and a good stand of flowers was obtained from all boxes, with no obvious difference between those known to be affected and others unaffected when taken into the glass house.

The close relation existing between soil and weather conditions and attack by *Pythium* was confirmed in 1939, when this fungus was recognized for the first time as the cause of serious loss among tulips that had been grown in the open. The disease occurred on a nursery in Buckinghamshire, where the soil is in part a heavy, binding loam, in part a light loam on gravel and in part intermediate in nature.

The weather in the district was cloudy, cool and dry for some weeks until mid-July, but rain, at times heavy, fell almost every day from then until about 10 August. Subsequently there was a hot, dry spell with day temperatures of 21–24° C. in the shade until 24 August.

On the nursery in question tulip lifting is normally begun in mid-June and finished by mid-July. In 1939, however, owing to the hard condition of the soil, few bulbs were lifted before mid-July and the operation was not completed until early August. Each day the bulbs that had been dug were taken to sheds for cleaning prior to storage. Growth during the season had been normal and the disease was not observed until the bulbs were being cleaned, and then only in those lifted after the wet weather had begun. The amount of disease was negligible in the stocks grown on the light soil and although more was present in those from the medium loam it was only in stocks taken from the heavy land that severe loss was experienced. Prince of Orange was the most susceptible of the varieties grown, and nearly 20 % of the bulbs of this variety grown on the heavier land had to be discarded, while the same stock on the lighter soils yielded very few diseased bulbs. Other affected varieties were Duchess of Hohenberg and Paul Eudel on the heavy land, Formosa and La Merveille on the medium soil and Purple Celeste on the gravel.

The disease was undoubtedly aggravated by the hot spell of weather in August, for in some stocks many slightly infected bulbs, overlooked during cleaning on 14 August, were brown and soft four days later. These were removed and, once day temperatures had fallen, little further trouble was experienced.

The badly affected bulbs were brown, soft and rubbery or reduced to a slimy, dirty yellow mass. The internal parts of others were still white and sound, but the outer fleshy scale was wet, soft and sticky, and dull white or pale yellow-brown, often with a well-marked yellow or brown line between the healthy and diseased parts. Slightly attacked bulbs showed partial or complete rotting of the basal plate and of the young bud within the bulb. Species of *Penicillium* and *Fusarium* sometimes developed in profusion on the outer scales in the later stages of attack, but the only constantly occurring organism was *Pythium*, and two strains of this were isolated in pure culture. One of these exhibited the characteristic features of *Pythium ultimum* Trow; in cultures on oat extract agar its conidia measured 22–31 μ (average 25 μ) and oospores 16–21 μ, the latter with walls about 2 μ thick. The antheridia were mostly androgynous. The other strain did not produce sexual organs and could not be identified, though it resembled the form previously found in England under glass (Moore & Buddin, 1937). On the whole its conidia were slightly smaller (21–28 μ in diameter) on oat extract agar than those of *P. ultimum*.

In late September a dozen healthy Prince of Orange bulbs were

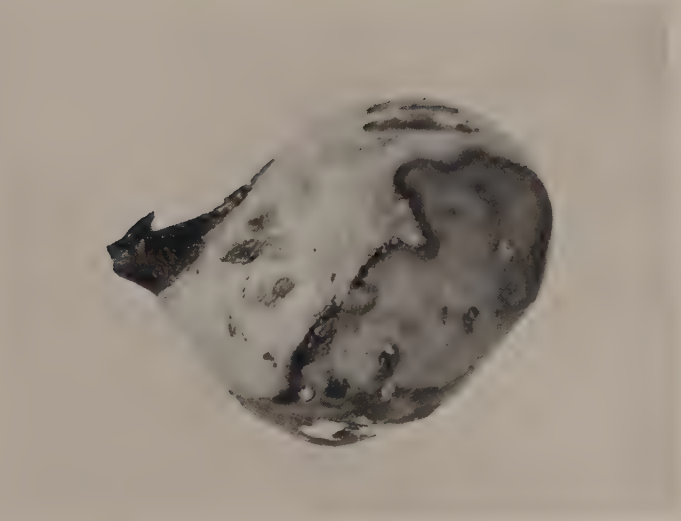

Fig. 2

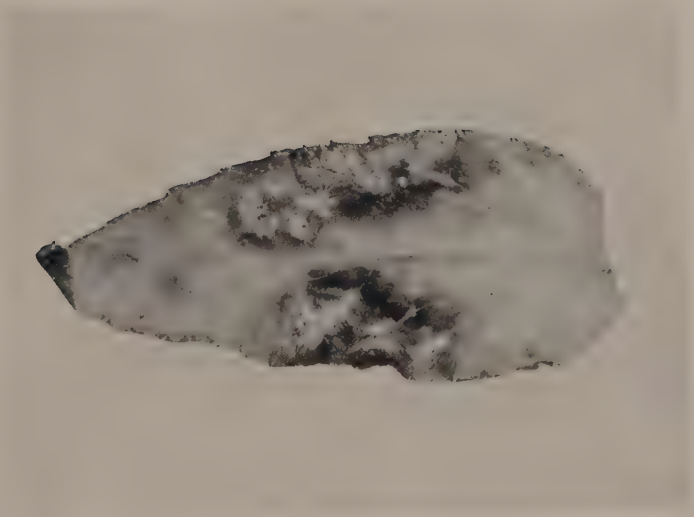

Fig. 1

inoculated with pure cultures of one or other of these two strains, through wounds made in the basal plate, and the bulbs were left standing on about $\frac{1}{8}$ in. of water on the bottom of closed glass dishes kept at 22° C. Within four days both strains of the fungus spread rapidly through the bulbs; these all became soft and rubbery and closely similar in appearance to bulbs naturally infected (Pl. III, fig. 2). Others treated in the same manner, except that the fungus was not inserted into the wounds, remained sound. A second batch of inoculated Prince of Orange bulbs was placed in dry, open glass dishes kept in an unheated room. After a fortnight, during which the temperature ranged from 7–14° C., the greater part of one bulb had become soft and rubbery and three others exhibited slight rotting of the young bud and adjacent scales, but the remaining six bulbs and the uninoculated controls were still sound.

When bulbs slightly or moderately attacked by *Pythium* rot were kept in cool, airy sheds on the nursery the disease was soon checked. The affected parts remained brown and relatively soft, or the outer scales or the whole bulb became white and chalky or hard and calcified. It then became extremely difficult to demonstrate the presence of the *Pythium* in the tissues, and the appearance of the bulbs was typical of Chalking (Chalkiness), a condition which appears to be the final stage in a series of changes, induced by several different parasitic or non-parasitic causes (Moore, 1939, p. 41). Chalking had been noticeable among stored bulbs at this nursery in previous years, especially in 1935 and 1938, and most of it may well have been a result of attack by *Pythium*. The only previous occasion on which the *Pythium* was actually observed in association with Chalking, however, occurred in August 1938, when it was isolated from soft rotten tissue at the base of one or two affected bulbs of Paul Eudel.

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EXPLANATION OF PLATE III

Fig. 1. Leaf of *Lobelia syphilitica nana* (enlarged) attacked by *Septoria Lobeliae* Peck.

Fig. 2. Prince of Orange tulip bulb artificially infected with *Pythium* rot. Inoculated 27 September 1939. Kept four days at 22° C. and then left in open dish on laboratory bench until photographed on 16 October.

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SOME PROBLEMS OF COLLECTING LARGER FUNGI IN THE TROPICS

By G. B. MASEFIELD, M.A., A.I.C.T.A.

The object of this paper is to draw attention to some of the difficulties, which may not be realized by mycologists in Britain, experienced by collectors in tropical countries; and to discuss ways in which the situation might be improved. Amongst these will be included co-operation by mycologists and institutions at home.

Let us consider first the outstanding features of the larger fungus flora which has to be studied. The remarks which I shall make are based on some experience of collecting in the West Indies and in Uganda. Both these territories are marked on vegetational maps as areas of "moist tropical rain forest". In face of the picture of luxuriant vegetation which this conjures up, the newcomer is surprised to find that even in the forests of these countries the larger fungi are less noticeable in numbers than in an English wood in autumn. This applies particularly to the ground species of saprophytes; parasites on trees and bracket forms on old wood are more abundant, and are probably as plentiful as in the British Isles.

If we turn to the grassland and scrub zones outside the forests, the paucity is even more striking. True grassland species appear to be distinctly rare, a large number of the fungi which are found in these situations turning out on closer inspection to be coprophilous or growing on buried wood. An interesting point in the vast areas of short-grass plains in East Africa is that coprophilous fungi appear chiefly on the droppings of two animals—cattle and elephants. The latter is a particularly rich substratum, and as there are some 20,000 of these beasts in Uganda this is quite an important ecological site! The dung of buck and other game carries far fewer of the larger fungi.

To this general scarcity must be added the fact that there are prolonged dry periods in Uganda during which large fungi other than wood-growing species are very hard to find. The amateur collector is further discouraged by the fact that few of the tropical fungi are large or of striking appearance; the majority are small, dull-coloured, and not of the genera which are most easily distinguishable. The absence of some of the most striking genera which occur in temperate Europe is rather remarkable. In five years in the tropics I have not collected a *Boletus*, a *Lactarius*, or a *Russula*. Amongst other genera of representative groups which do not seem to occur are *Amanita*, *Morchella*,

Dacryomyces, and many of the less common British genera. In compensation for this, it is only rarely that one collects a fungus which is undoubtedly of a non-British genus.

These facts open up the first lines of research, which must be ecological. Why is there this paucity of individual fungi, and possibly also of species, in at least some tropical countries? Two solutions immediately suggest themselves. The first is that climatic conditions, and particularly rainfall, may be unsuitable. Most parts of Uganda have an average annual rainfall of something like forty or fifty inches, which is not high for a tropical country; and this may be unfortunate for the fungus collector. Some support is lent to this view by the fact that in the forests of the Sese Islands in Lake Victoria, with an average rainfall of some eighty inches, large fungi are particularly abundant; this applies in a lesser degree to the other forests of the lake region, some of the fungus flora of which has been listed by Maitland & Wakefield (*Kew Bulletin*, 1917). On the other hand, fungi are not particularly abundant at high altitudes on the mountains of Uganda, where conditions are cooler and moister than in the plains and more like those of Europe. It is true that at one season of the year I found large fungi rather abundant in the bamboo forest of the Mufumbiro volcanoes in south-west Uganda; but my general impression is not one of abundance, and in the forests of Mount Elgon I have not found many fungi.

A second possibility is that in these regions the ecological competitors of the larger fungi—bacteria, moulds, termites and other insects—destroy the available substrata too quickly for these fungi to get a hold. The termites may, I think, be ruled out because fungi are not noticeably more abundant above altitudes of about 6000 ft. where termite depredations are rare or absent. The other possibilities require investigation, and a microscopic study of mycelia and structural decay in rotting humus from tropical forests might yield results of great interest.

Another quite different line of ecological research might be based on the non-appearance in tropical floras of common European genera, as mentioned above. A linked study of intermediate regions such as the Near East might perhaps give the key to the geographical distribution of some of these fungi.

Another aspect perhaps worth investigation is the edible qualities of local fungi, many of which are eaten by native tribes. A list of thirty or forty such species with distinct names in various native languages of Uganda can be obtained without any difficulty.

Let us now turn from the ecological to the systematic aspect. Here the newcomer to a tropical country finds his chief difficulty in the lack of any available literature and of records of previous collections. In Uganda the Government Mycologist has collated a list of Hymeno-

mycetes so far recorded in the country, which comes to a total of 224 species, of which a few are synonyms. Many of these species are described in publications which are difficult to obtain, and for some of them there is actually no description available in the country. This list, as would be the case in most tropical countries, had grown in a very haphazard way; within a few months of arriving in the country I had collected such well-known species as *Psaliota campestris*, *Lepiota procera*, and *Laccaria laccata*, none of which genera had been recorded in Uganda before.

This instance will serve to show both the difficulties and the scope which lie before the tropical collector. I will illustrate further by reference to the genus *Lepiota*, which I have recently had occasion to study. This is a most useful genus for distribution studies, since it seems to be represented by fairly numerous species all over the world.

Saccardo in *Sylloge Fungorum*, vol. v, lists 186 species of this genus, and there are further species in the supplementary volumes. Rea lists 68 species from Great Britain; Velenovsky 46 for Czecho-Slovakia; Saccardo 55 for Italy; Migula 57 for Germany; Murrill 85 for North America, including Mexico and a few records from the Caribbean area. It is interesting to compare with these the longest lists which I have been able to find for tropical or semi-tropical countries. Berkeley & Broome originally in 1871, listed 68 species from Ceylon and more may have been added since as Ceylon has been one of the parts of the tropics best explored mycologically (e.g. Petch's long series of records in all groups, including many Hymenomycetes). Butler & Bisby give 29 Lepiotas for India; van Overeem-de Haas only 5 for the Dutch East Indies. Rick gives 92 for Brazil, of which 17 are new species.

A further point of interest is to compare the numbers of species common to both temperate and tropical zones in the above lists. Taking first the lists for the Old World, there are twelve species common to both temperate and tropical zones excluding Ceylon; for the New World, there are ten species common to North America and Brazil. These figures are of interest as showing how large a proportion of the tropical species are not included in the temperate floras; most species which are not so included being doubly difficult to find in books which are likely to be available.

Having indicated some of the difficulties which meet the collector in the tropics, let us consider what might be done to remedy them. A central body at home might help a great deal by collating a list of larger fungi which have already been identified in British tropical dependencies; such a list, however, will lose half its value if it is confined to a restricted group such as the African colonies (for which the idea of a list has been suggested before), and if descriptions of the species are not included as well as records. The existence of such a list

would probably lead to the filling of many gaps in the flora of individual territories.

Even with such aid, however, there will remain a large number of species which cannot be identified either in the field or at the capitals of most Colonies. Such species have to be sent to Europe before their identity can be determined. For a certain number of bracket forms and tough fungi it is possible to do this, with the result that such groups at present dominate the lists of recorded fungi in many tropical countries. But even with these species there are difficulties. The identifications often take months to come back from Europe, and meanwhile the duplicate specimens which have been kept by the collector in a moist tropical climate have succumbed to the attacks of moulds or insects. The keeping of large specimens preserved in fluid is not satisfactory either for the structure of the fungus or for the amount of space and preservatives required.

There remains a vast majority of the larger fungi which cannot be dried. The best that can be done with these at present is to make careful notes and drawings, with material in preservative, and a sketch to show the fresh appearance; the drab colours and small size of most tropical species do not lend themselves to the assistance of the amateur artist. Such notes should, however, enable a collector to recognize a species when he collects it for a second time. It seems to me that by this means it might be possible, at the capital of a Colony, to keep records under tentative names of many fungi which cannot at present be definitively named. For example, any species collected locally and for which a clear description with drawings was available might be listed as "Probable Genus X—No. Y"; and this number and notes would be available for use by later collectors. Thus considerable ecological knowledge might be amassed about a species whose systematic position was still uncertain; and at a later date a name could be given to it.

This would most easily be done by a visiting expert; and such visits are the last point which I wish to advocate for the assistance of tropical mycology. There is no doubt that our knowledge of many tropical floras might be enormously increased by visits from expert mycologists, especially those versed in specialized groups; is it too much to hope that such visits might one day be sponsored by a body such as the British Mycological Society? They would do much to loosen the Gordian knot which is at present hampering our advance in knowledge; that the man on the spot makes repeated collections of common fungi which he cannot identify, and the expert who could identify them cannot see them.

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A LIFE CYCLE OF *BLASTOCLADIA PRINGSHEIMII* REINSCH.

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(With 9 Text-figures)

Introduction

To students of the Phycomycetes perhaps the most interesting work of recent years is that of Kniep (1929) on the water mould *Allomyces javanicus*. When he announced that this fungus produces two kinds of motile gamete, a micro- and a mega-gamete which fuse to originate a zygote, he described a phenomenon unique among the fungi. Isogamy was known among many chytrids; so were the oosphere and motile microgamete of *Monoblepharis sphaerica*; but the heterogamy of flagellate gametes was new. His further description (1930) of an alternation of generations—of a sporophyte with a gametophyte of similar appearance—intensified mycological interest.

Butler (1911) founded the genus *Allomyces* on *A. arbuscula* and included it with *Blastocladia* in a group Blastocladiaceae, chiefly on the character of the resistant sporangium and the absence of cellulose in the hyphal wall. The two genera have other features in common, viz. the vegetative part of the thallus mainly rhizoidal; the reproductive part with a stout main axis, bearing more slender branches; and thin-walled sporangia, bearing zoospores with one posterior flagellum.

The genus *Allomyces* thus brought into prominence has been intensively studied since Kniep's discovery. Emerson (1939) has suggested dividing the genus into three subgenera according to the different life cycles that have been observed, viz. *Eu-allomyces*, with alternation of equal sporophyte and gametophyte generation; *Brachy-allomyces*, without alternation of generations; *Cystogenes*, with encystment of swarmers.

Now although the genus *Blastocladia* has been known since Reinsch (1878) first described *B. Pringsheimii*, its life cycle has remained unknown.

Nearly twenty years later, Thaxter (1896) rediscovered the genus, described it more fully, and established a second species. Since then von Minden (1916) has published a morphological account of the group, adding two species; Cotner (1930), a cytological investigation of the zoospores; and Lloyd (1938), a comparative study of the vari-

able thallus of *B. Pringsheimii*. Otherwise there have only been records of the genus in various parts of the world, and the description of four or five new species.

The sporangia of Blastocladia

In spite of the recent claim made by Bessey (1939), it seems certain that, as in *Allomyces*, the swarmers from the thin-walled sporangia of *Blastocladia* spp. do not fuse. During the two years 1933–5, at frequent intervals, Lloyd (1938) watched swarmers liberated from these sporangia but never saw fusion: on the contrary she observed direct germination of the individual swarmers.

The morphological significance and function of the resistant sporangia (Fig. 1) have so far been a matter of conjecture (Blackwell, 1939).

Reinsch (1878) described these thick-walled resistant bodies as doubtful oospores, for they can slip out of their outermost thin wall which remains behind on the thallus. Kanouse (1927) accepted them as such and claimed that she had found an antheridium. Thaxter (1896), however, rightly compared them with the resting conidia of the Pythiaceae.

The secret of the life cycle lay with these resistant sporangia which had always defied germination in culture. Lately, it had been assumed that, on germination, they would liberate swarmers as in *Allomyces*, for the resistant sporangia of both genera resemble one another so closely in occurrence and in form, and are unlike those of any other fungus except the newly discovered genus *Blastocladiella*.

But what the swarmers, thus liberated, would become was quite unknown. When, therefore, abundant germination of the resistant sporangia of *Blastocladia Pringsheimii* was obtained in 1937, the fate of the swarmers was closely watched.

Source of the material

The plants of *B. Pringsheimii* used in this study were obtained from a tank in the greenhouse of the botanical garden, Royal Holloway College, and cultivated there and in jars of tap water in the laboratory, on tomatoes, grapes and other thin-skinned berries.

About a month after inoculation of the fruits, the fungus usually bore abundant resistant sporangia (Fig. 1 *a*); and these were germinated not less than three months later.

The fruits, or merely the skins of the fruits, bearing the colonies of fungi with resistant sporangia, had meanwhile been stored either in water, or between layers of plain agar, or, occasionally, dry. It was found essential that the resistant sporangia should be thoroughly ripe

before being stored, and that if stored dry, they should be dried slowly.

Formation and fate of the resistant sporangia

Time of appearance. Thin-walled sporangia always appear first. Exactly what causes the formation of resistant sporangia among the

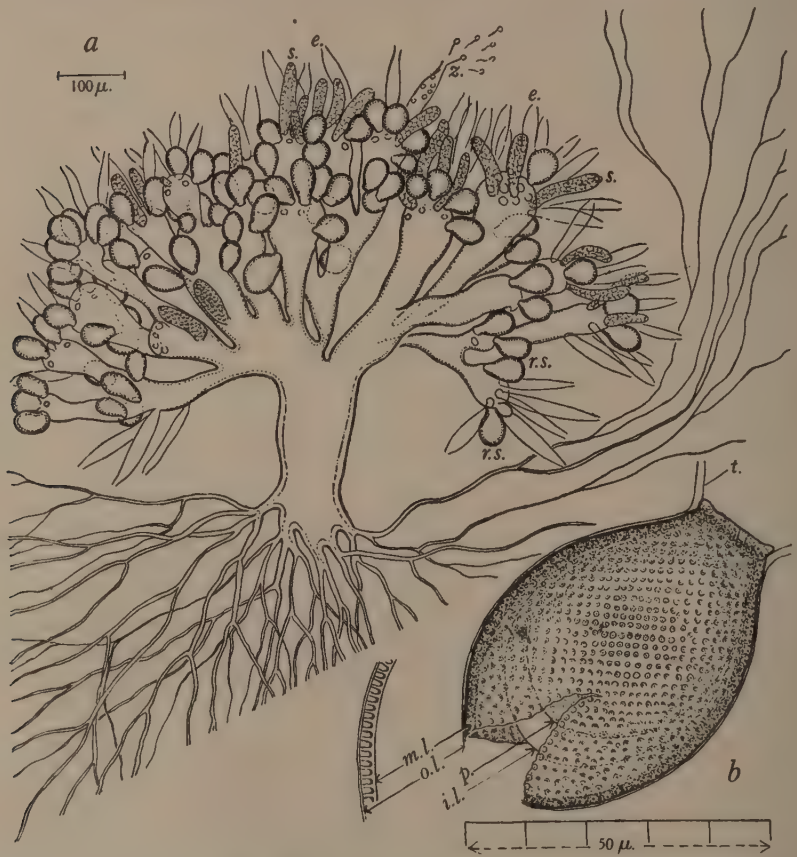

Fig. 1. (*a*) A plant of *Blastocladia Pringsheimii* Reinsch with far-reaching rhizoidal mycelium (only a part of this shown), and stout emergent trunk and branches bearing both resistant sporangia (*r.s.*) and thin-walled sporangia (*s*) some (*e*) emptied of the uni-flagellate zoospores (*z*). (*b*) A dried resistant sporangium cracked open and showing the three wall layers: the outermost (*o.l.*) continuous with the thallus wall (*t.*), the middle (*m.l.*) thickened and pitted (a portion is shown in section), and the innermost (*i.l.*) intact and somewhat withdrawn enclosing the still further contracted protoplast (*p*).

thin-walled sporangia is not known. The thallus must attain a certain age before producing them: thalli less than six days old have

never been found to bear them; on the other hand they may be eight or more weeks old and still not bear them. It seems that the fungus at all seasons may, or may not, produce them, and thalli grown under apparently similar external conditions behave differently.

Initiation. Resistant sporangia are initiated in much the same way as are thin-walled sporangia, and, until a cross-wall is formed at the base, neither sporangium can be distinguished from a young vegetative lobe of the thallus. The fact that a resistant sporangium can, rarely, be branched gives support to this close comparison with a vegetative lobe. The initials of all three are very soon multinucleate. Development begins very rapidly and the appearance of a cross-wall is the first distinguishing sign of sporangium formation. Simultaneous mitoses follow. Later the shape of the sporangium and the character of the wall distinguish the two kinds of sporangium.

Shape. The resistant sporangium is typically short and ovoid, whereas the thin-walled sporangium is long and cylindrical, but both types show a wide range of form. The exceptional occurrence of long cylindrical resistant sporangia suggests that the final character of the sporangium may be determined at a late phase of development.

Contents. The central vacuole is common to both types but is used for a store of fatty reserve material in the resistant sporangium.

Wall. The resistant sporangium develops the characteristic thick and pitted wall, while the other type develops a characteristic papilla just within the apex.

The wall of the resistant sporangium is three-layered (Fig. 1*b*):

(1) The outermost layer continuous with the thallus wall—the original wall and comparable with the wall of the non-resting sporangium.

(2) The middle, thickened, pitted layer.

(3) The innermost, a layer clearly seen on germination when it protrudes through a split in the thickened wall (Fig. 2). It is thin and extensible.

The thickened layer is often called the exospore, as in *Allomyces*, where the resistant sporangium usually slips out of the outermost layer which then appears like an investment or sac. In cultures of *Blastocladia Pringsheimii* however the resistant sporangium remains on the old thallus, or finally separates only by the rotting away of the old thallus below. It can, however, slip out of the investment and perhaps in nature it normally does this. The thallus wall forms a stiff collar in which the resistant sporangium is set.

Chemical nature of the pitted layer. The characteristic pitting of the middle layer, observed and figured by both Reinsch and Thaxter, is evident at a very early stage of development and forms quickly. It appears to be brought about by minute, round, regularly arranged areas on the outer face of this layer developing into some easily dis-

organized substance; while the rest, in honeycomb pattern, changes into a very resistant protein which gives some reactions for keratin, e.g. it stains pink with Millon's reagent and yellow with picric acid. There is no cellulose or fat in the wall and it is not chitinous. (Parallel observations and tests made on the middle layer of resistant sporangia of *Allomyces javanicus* and *A. arbuscula* have shown that although this layer is thicker than in species of *Blastocladia*, it does not give such a strong reaction for protein, e.g. it does not give such a definite pink colour with Millon's reagent. It may be that the different chemical nature of this layer explains the more resistant nature of the resistant sporangia of species of *Blastocladia*.)

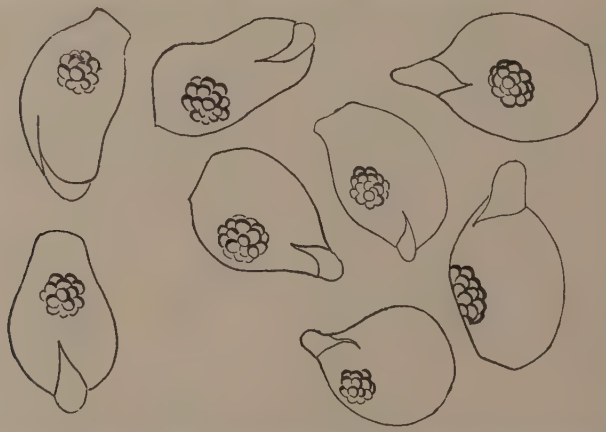

Fig. 2. Outline drawings of resistant sporangia in the first stage of germination. The shape of the sporangium is more or less ovoid. The groups of oil globules, the slit at the apex and the protruding innermost wall layer are constant features at this stage. The two on the left were found in May, stored in June, soaked 12 October and germinated 14 October 1938. The rest were found in May, stored in June, soaked 7 November and germinated 8 November 1939. The readier germination of older sporangia has been demonstrated on many other occasions. Magnification as in Fig. 3.

Distribution of pits. Since Emerson (1938) has shown that in *Allomyces*, the size and distribution of the pits is a useful diagnostic character in determining species, it is perhaps important to record that the pits of the resistant sporangia of *Blastocladia Pringsheimii* are about 2μ apart; there are as a rule five or six pits to 11μ, the outside limits being four and a half to seven pits.

Germination of resistant sporangia

The resistant sporangia of *B. Pringsheimii* are notoriously resistant to attempts to induce germination, and the first record of successful germination occurs in a letter to *Nature* in November 1937.

After this announcement was made (Blackwell, 1937), it was found

that von Minden (1916) had illustrated three cracked resistant sporangia, each with papilla emerging; he stated, however, that he did not see swarmers liberated, although he saw them outlined within the sporangium. Later it was learned that in February 1937, Emerson had not only germinated resistant sporangia of *B. Pringsheimii* but had also cultivated the germlings from the liberated swarmers. He had not, however, recorded this, and so it was not generally known.

Conditions of germination

It is not possible as yet to give precisely the conditions required for germination. Like so many resistant spores of fungi, out of a great number, treated apparently just alike, a few now, and a few later after different intervals, will germinate. Undoubtedly spores vary among themselves in thickness of wall, in size and in quantity of reserve material.

But certain general facts have been established about resistant spores and sporangia:

(1) They must be thoroughly ripe before they are stored; and they may then be stored wet or dry.

(2) They require a period of "after-ripening", the length of which no doubt depends in part on temperature: the resistant sporangia of *B. Pringsheimii* have not, as yet, been germinated under three or four months without special "coaxing".

(3) One form of "coaxing" is to subject the mature spores to periods of alternating dry and wet conditions and to periods of alternating heat and cold. Mechanical, physical and chemical factors all play a part in cracking a thick wall.

(4) *To induce germination*, water is essential. It is assumed that oxygen is essential too but it is an immeasurably small amount. The oxygen dissolved in the water-film under a coverslip is adequate.

(5) *To control germination*, it is advisable to store the spores almost dry because in water they will ultimately germinate spontaneously, one at a time, and as by that time they have dropped from the old plant it is not easy to find them.

These sporangia are not only resistant but accommodate themselves to the environment. If right conditions for germination do not arise they can continue resting for months; if right conditions are interrupted they can resume a resting state. A high percentage of germination has been obtained in resistant sporangia kept under a coverslip for nearly seven weeks, sometimes wet and sometimes dry.

Germination

When ready to germinate, the resistant sporangium has a group of oil globules, balled in the centre (Fig. 2). This is a sure sign of active preparation for germination. It is no doubt the result of the breaking

up of the fat vacuole. The rest of the protoplasm is clear and transparent.

The thick, pitted, middle wall-layer cracks across the apex, and the thin innermost layer, now exposed, stretches to accommodate the swelling protoplast within. By and by a small papilla develops (Fig. 3): less frequently two papillae (Fig. 4).

The resistant sporangium may remain thus for several hours with no external change except perhaps a further swelling causing a larger bulge of the innermost wall, but with considerable internal change. It may go no further than this. Under favourable conditions, however, it liberates swarmers twelve hours after the fresh water is first supplied to the resistant sporangium.

Formation of the swarmers

Just before the multinucleate protoplast is cut up into swarmers, the cluster of oil globules disperses throughout the protoplasm and the resulting smaller globules are included unequally in the swarmers. At this stage the resistant sporangium, with the unequal and irregularly distributed globules, looks not unlike a resistant sporangium that has disorganized. But within a few moments the swarmers are formed and can be seen heavily moving on one another (Fig. 3).

Emission of the swarmers

Then the papilla gives way. If there are two papillae both may dissolve together (Fig. 4*b*). A few swarmers pass out and are held for a moment in what might be interpreted as a quickly evanescent vesicle, and then break free and roll slowly away. The rest of the swarmers (forty or thereabouts according to the size of the resistant sporangium) then squeeze through the small opening left by the dissolved papilla—one, two or three a minute. The sporangium may be emptied in fifteen minutes or take as long as an hour.

Each swarmer moves freely within the resistant sporangium until impelled towards the opening. In the early stages of emission swarmers crowd to the opening and sometimes attempt to push through two together (Fig. 3). As soon as one is through there is another pressing into the opening. In the later stages they charge the opening, attempting to get through, even when only one or two are left and yet they always squeeze through with an effort. They are of different sizes and contain by chance different quantities of oil globules.

The emission of swarmers is not unlike that from the thin-walled sporangium but measurements indicate that they are larger.

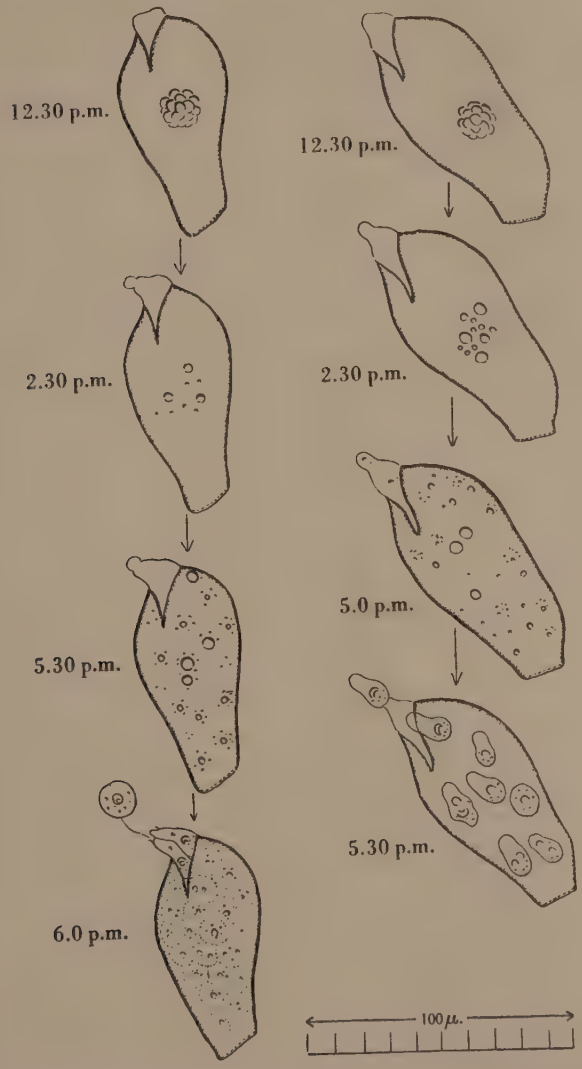

Fig. 3. Successive drawings of two resistant sporangia under observation during germination from 12.30 p.m. to 6.15 p.m. 16 February 1939. Stages in germination shown: the cluster of oil globules disperses; the papilla forms; movement of oil drops reveals great activity of protoplasmic contents; the protoplast is cleft into spores; the papilla dissolves, and appears to be continually re-formed by the pellucid (non-flagellate) end of each next emerging swarmer; the spores escape rapidly (in the right-hand one the last few emerged slowly: the left-hand one was emptied in fifteen minutes).

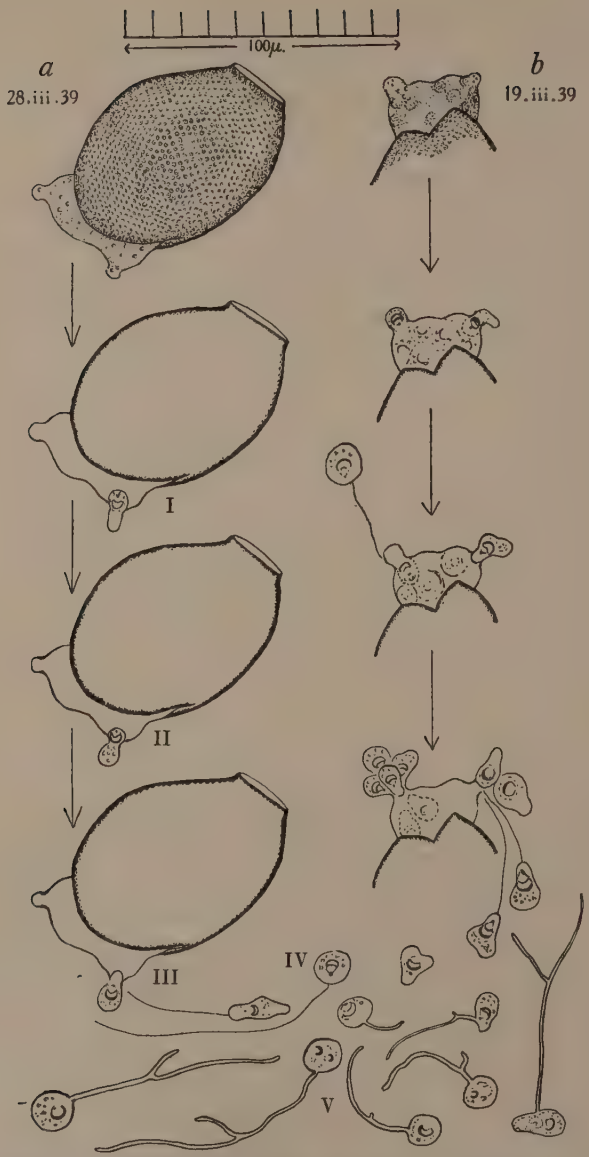

Fig. 4. Successive drawings of two sporangia, each with two papillae, under observation during germination on 19 and 28 March 1939. In (*b*) (only apex shown) the two papillae dissolved almost simultaneously and emitted swarmers together. The earliest swarmers to emerge appear to replace the papilla. A pellucid pseudopodium appears at the orifice and swells (I). Tiny oil globules surge into it until the more fluid cytoplasm of the swarmer has passed out (II). Then with an effort the more solid nucleus is discharged into this projecting part of the swarmer (III) and the swarmer is free (IV). Later swarmers escape more easily and several may attempt to push through the orifice together (*b*). Swarmers are often held awhile at the orifice by the flagellum. They may become amoeboid while straining to escape. Germination (V) follows immediately.

The swarmers free

Once free, the swarmer often lies quiescent recovering the spherical shape which it bore within the resistant sporangium, but lost on squeezing through. It then begins to quiver as the flagellum comes into play. The flagellum sometimes catches in the opening and holds the swarmer, straining to escape, which it finally does with a quick movement. But if not caught, the swarmer slowly, softly rolls away, with a forward spiral movement, and a little later swims actively along, always, however, with a rolling motion, and with the flagellum trailing behind. The swarmer by this time is slightly elongated and in its free-swimming state is ovoid.

Under exceptional circumstances the swarmers have an amoeboid phase immediately on emission. The active swarmers may remain active for a day, with periods of amoeboid form and movement. These amoebae have a clear ectoplasm and change their form rapidly: almost too rapidly for the pencil to record. The amoeboid state can be changed to the swimming state by the addition of water.

GERMINATION OF THE SWARMERS

After a day or less, the ovoid swarmer ceases motility and settles down as a spherical unicell and puts out a thin germ-tube. This is the rhizoidal hypha which after growing to several times the length of the spore puts out an equally thin branch. Only after this long, branched, rhizoidal hypha has developed does the body of the swarmer swell and the nucleus divide. It grows into a characteristic horizontal club-shaped hypha which is the sporangium-bearing part of the thallus. It may bear a sporangium at once or only after further growth and branching (Figs. 5, 7, 9).

Naturally occurring germlings from resistant sporangia swarmers may be found established in a bed of bacteria or at the edge of a morsel of vegetable matter. They have been grown to maturity in three artificial habitats: (1) in a jar of water, in mass cultures on the surface of tomatoes, (2) on microscope slides, under a coverslip ringed with corn meal agar, (3) in Petri dishes, in pure culture on corn meal agar.

(1) *Plants on tomatoes.* Resistant sporangia in abundance, with the characteristic cluster of globules and the papilla just formed, were added to water with small tomatoes, or alternatively, swarmers, just liberated in hundreds, were added.

After two days the characteristic pustules could already be detected by the naked eye, indicating the presence of colonies of mature plants. These plants liberated swarmers which did not fuse. Assuming that there was, as in *Allomyces*, a gametophyte generation, it became clear that already the sporophyte had formed, so one looked earlier.

Germlings were sought and found as early as twelve hours after the swarmers were introduced into water with the tomatoes.

It was impossible to see anything on the living skin after less than one day, but when the epidermis was peeled off, fixed in 4 % formalin, stained in cotton blue and examined closely under high magnification tiny plants were found "rooted" in a cuticular crack or an old hair base. A scraping of the skin, similarly treated, revealed them but not *in situ*.

These tiny plants were of two kinds:

(*A*) solitary, small flat thalli, dichotomous, with blunt sporangia often already emptied, and the body of the thallus nearly always empty (Fig. 5);

(*B*) groups of germlings, often eight in a group, either very young and still uninucleate or older (Fig. 6).

In both (*A*) and (*B*) the rhizoidal part of the thallus was extensively developed within the mesocarp of the tomato.

The relation between these two types of growth was difficult to interpret. They both appeared very soon after the germination of the resistant sporangia. The resistant sporangia would liberate swarmers about twelve hours after emission in water; groups of germlings have been found eighteen hours later; solitary thalli have been found twelve hours later. But these latter are difficult to find, except when resistant sporangia are germinating in abundance. It is highly probable that the solitary thallus (*A*) precedes the group (*B*). Fig. 5 (inset) is very suggestive of this. Here is an empty flat thallus in an old hair base and on the same exposed cellulose wall is a group of germlings. Have these come from a sporangium of the flat thallus, for this might give several groups within an hour? It is significant that on tomato skins where such groups have been found there are wide areas bearing nothing at all.

(2) *Dwarf plants in slide cultures.* It was later discovered that swarmers would germinate and grow to maturity with a minimum of oxygen under a coverslip. These were nourished and kept moist by a ring of corn meal agar around the coverslip. The oxygen available was in solution in the water film, and so scarce that infusoria could not live in it. The thallus formed under such conditions is *minute*. The mature dwarf plant retains the size and form of a germling, and produces the first sporangium so soon as the branched rhizoidal hypha has developed and "rooted" it in some morsel of vegetable matter. The sporangium emits four or eight swarmers which have never been seen to fuse (Fig. 7).

As a result of interrupted emission of swarmers from resistant sporangia in slide cultures (due to temporary lack of water, and possibly of encystment of swarmers), such dwarf individuals have been

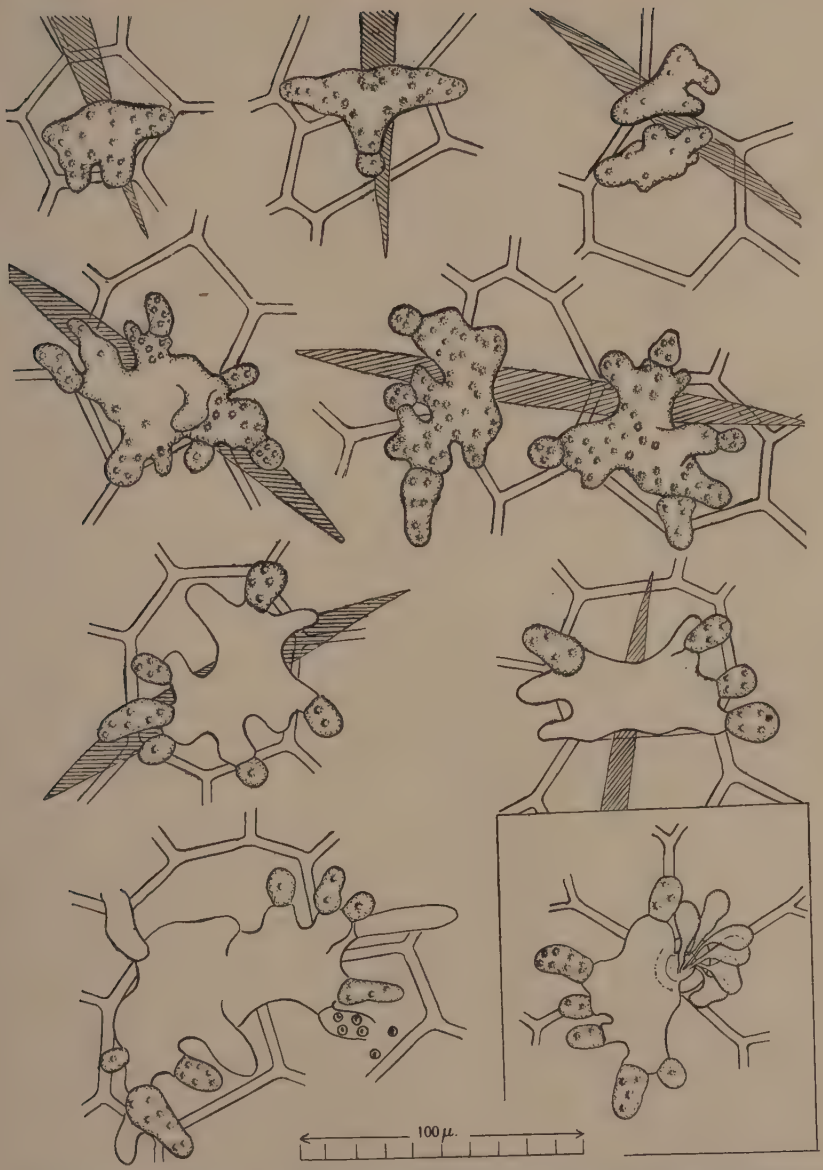

Fig. 5. Solitary flat thalli—not more than two days old and not as large as an epidermal cell of the tomato on which they were growing—found established, 19 September 1938, in a cuticular crack of the epidermis. Three of them, rather older than the rest, have evacuated their protoplasm into the sporangia, leaving the body of the thallus empty in characteristic fashion. (Groups of germlings as shown in Fig. 6 were present elsewhere on the surface of the same tomato.) *Inset*. A similar solitary thallus—not more than two days old—found established, 4 November 1938, in an old hair-base, and, with it, a group of six germlings (cf. Fig. 6), possibly from one of its sporangia.

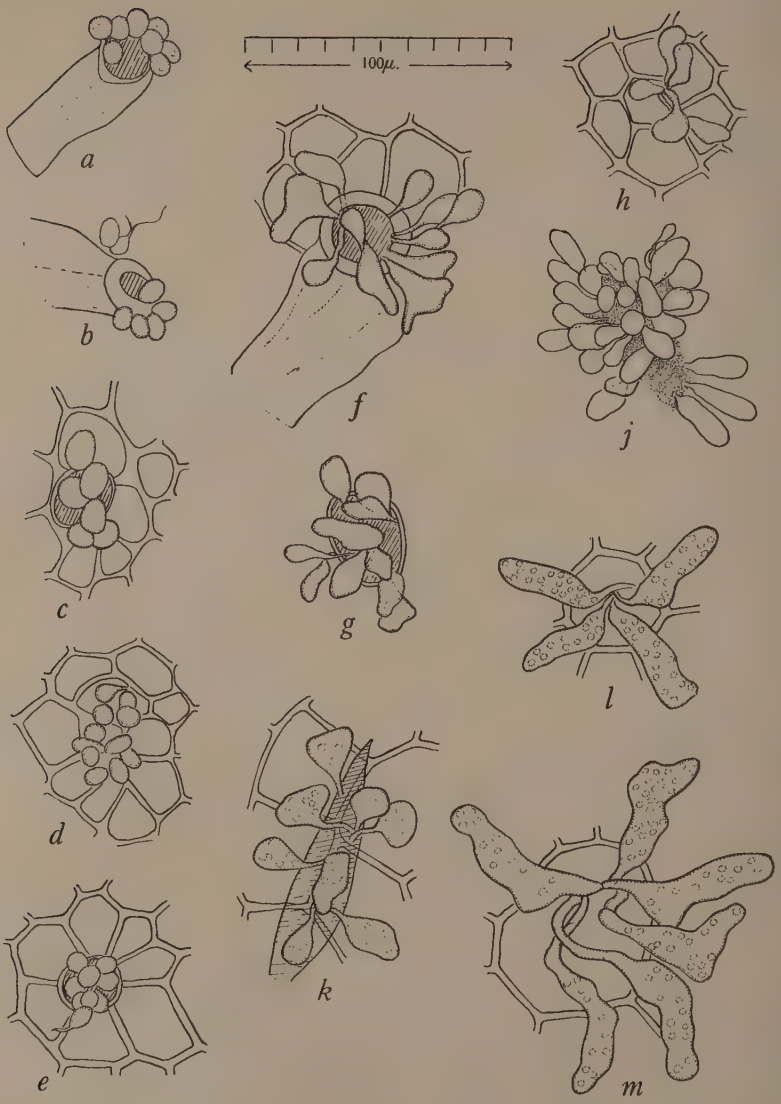

Fig. 6. Groups of germlings, less in size than the epidermal cells of the tomato on which they were found growing. (*a*)–(*e*) 15 October 1938. Five groups found—eighteen hours after stored resistant sporangia emitted swarmers—established in the base of a dead epidermal hair (wall of the hair shown in (*a*) and (*b*)). (*f*), (*g*) 4 November 1938. Two groups of older germlings found—not more than forty-eight hours after the stored resistant sporangia were dropped into water with a tomato—established in the base of a dead epidermal hair (wall of hair shown in (*f*)). (*h*), (*j*) 14 February 1939. Two groups found within sixty hours after stored resistant sporangia were dropped into the water with a tomato. Group (*j*) is in a bed of bacteria. (*k*) 2 November 1938. A group of eight germlings found—within twenty-four hours of putting soaked resistant sporangia into water with a tomato—established in a crack in the cuticle of the tomato epidermis. (*l*), (*m*) 6 October 1938. Two groups of older germlings (crack in cuticle not shown).

found at the mouth of the resistant sporangium and even within the wall (Fig. 8).

(3) *Plants on agar in pure culture.* Dr Ralph Emerson who had become interested in the work in progress, later applied his delicate

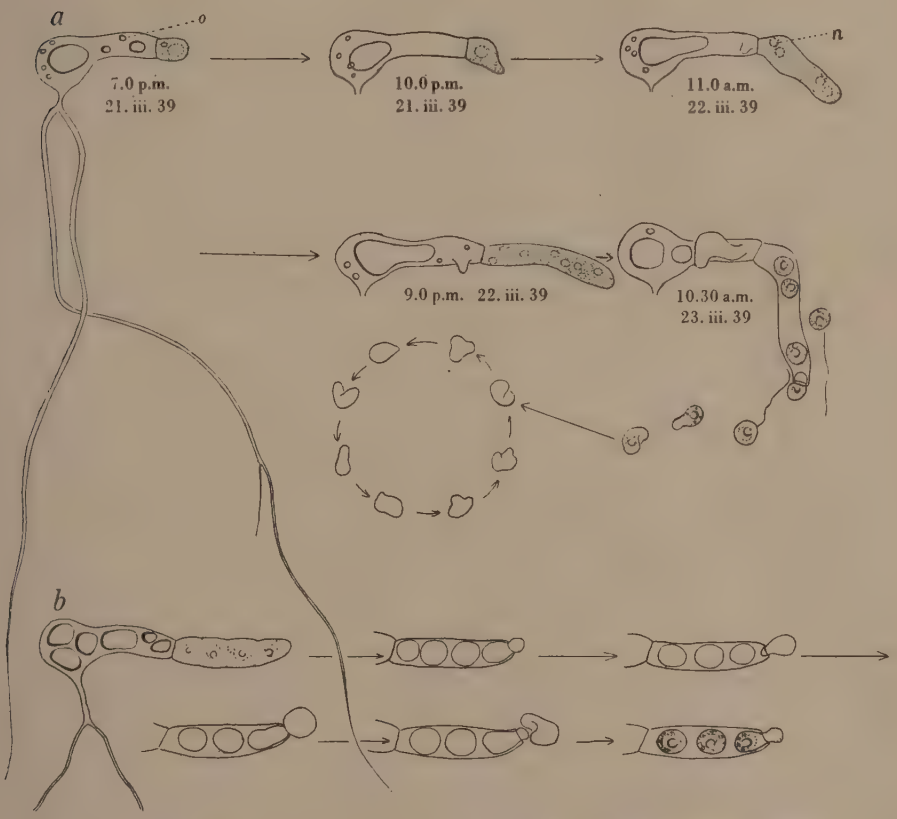

Fig. 7. (*a*) Five stages in growth of a plant derived from a swarmer from a resistant sporangium, and kept under observation under a coverslip from 7.0 p.m. 21 March 1939 to 10.30 a.m. 23 March 1939 by which time it had produced a sporangium with *eight* swarmers, and a second sporangium initial. The swarmers were liberated and became amoeboid. (*b*) Six stages in the development of a similar plant bearing one sporangium with *four* swarmers. *o*, oil globule; *n*, nucleus. Magnification as in Fig. 8.

technique for isolating swarmers, to this material. From an isolated resistant sporangium, just germinating, he isolated the swarmers and germinated them on corn meal agar in Petri dishes. They gave thalli with a profuse rhizoidal region and sporangium-bearing axes of the globose type with one or two dichotomies (Fig. 9). The swarmers

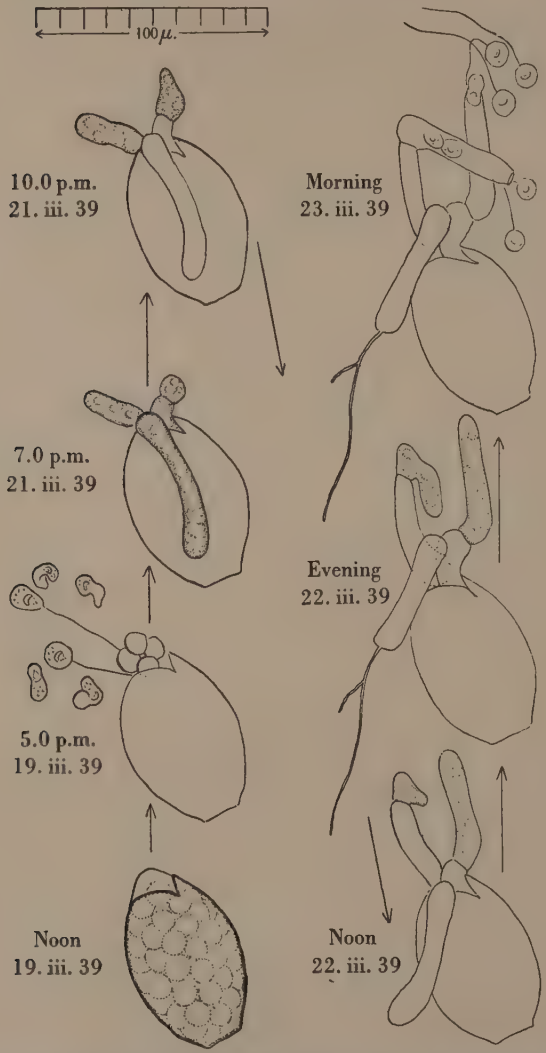

Fig. 8. Outline drawings illustrating seven stages in the germination of a resistant sporangium kept under observation under a coverslip from noon 19 March 1939 to morning 23 March 1939. The last three swarmers to emerge encysted at the mouth of the sporangium and later germinated there, each forming a sporangium and liberating four spores.

emitted by the sporangia of these plants were watched and fusion was never observed. The swarmers settled down and germinated, giving specimens not unlike the parents.

Fig. 9. Two plants from swarmers from resistant sporangia grown on sterile corn meal agar, 28 March 1939. (*a*) 30 March 1939. A two-day old thallus (seen from the side). One sporangium had emitted swarmers, which became germlings within an hour. (*b*) 4 April 1939. A seven-day old thallus (seen from above). Only the base of the very extensive rhizoidal system is here shown.

Conclusion

Gametes, if gametes there be, in *Blastocladia* have yet to be demonstrated. So far, one type of life cycle has been demonstrated involving no alternation of generations. It corresponds to the short cycle of Emerson's (1939) sub-genus *Brachyallomyces*, and Matthews's (1937) *Blastocladiella simplex*.

The thallus that develops from the resistant sporangium swarmer is variable and extremely accommodating, however, and it may yet be shown that it can, under certain conditions, produce gametes.

Summary

Although *Blastocladia Pringsheimii* has been known much longer than any species of *Allomyces* and *Blastocladiella*, its life-history has so far eluded discovery. This is partly due to the difficulty of inducing the resistant sporangia to germinate in culture.

A description of the mature resistant sporangium is given, especially of the structure of the thickened, pitted wall.

Resistant sporangia have now been successfully germinated on many occasions by ensuring first that they were fully mature. Practical hints are given for the encouragement and control of germination.

Phenomena of germination are described and illustrated: the cracking of the thick wall, the development of a papilla, the formation and emission of swarmers.

The fate of the swarmer is followed and its direct germination into a germling of characteristic form is described.

Germlings have been cultivated (*a*) on tomatoes in water, (*b*) in slide cultures, (*c*) on agar plates, and the mature thalli formed in these three types of culture shown to be quite different in form but always to liberate swarmers which have not fused but have germinated directly into groups of plants—the characteristic "pustule".

The life cycle here described corresponds with the short cycle of Emerson's sub-genus *Brachyallomyces* and Matthews's *Blastocladiella simplex*.

It is not suggested that another type of life cycle is impossible. *Blastocladia Pringsheimii* has shown itself to be of so variable a form both in nature and in culture, that it may well be variable also in its life cycle.

It is my pleasant duty to acknowledge the useful criticism and practical help generously given by Miss Grace Waterhouse and Dr Ralph Emerson towards the close of this investigation, and to thank Mrs Edmund Mason for kind help with the drawings.

APPENDIX

Tomatoes were chosen as "bait" for various reasons:

1. The epidermis is colourless.
2. The epidermis is easily torn off clean.
3. Minute cracks form in the cuticle when the tomato is lying in water, and the flagellum of swarmers is caught in the crack. The cellulose is here exposed.
4. There are old hair bases which likewise catch swarmers and offer exposed cellulose within.
5. The rhizoidal hypha of the germling readily penetrates the cellulose of the epidermal wall, thus exposed. (It has been observed that germlings do not settle on unhealthy tomatoes, with broken cell surfaces and they are slow to attack unripe tomatoes.)
6. Tomato skin is extraordinarily resistant. It remains in excellent condition in water for years.
7. When peeled off, the epidermis can be mounted conveniently,
   (*a*) outside up, to show the sporangium-bearing part of the thallus;
   (*b*) inside up, to show the rhizoidal part of the thallus.
8. The epidermis does not stain and remains as a yellow or colourless background to the artificially coloured germlings and plants.
9. Although epidermal cells vary in size in different varieties of tomato they are often useful in comparing size of germlings and grown plants.

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SOME FUNGI ISOLATED FROM PINEWOOD SOIL

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(With 1 Text-figure)

Attempts at the isolation of fungi from the soil began with the work of Adametz (1886), the earliest systematic account being that of Oudemans & Koning (1902). Since that time, many systematic studies of the soil flora have been made in many parts of the world, and the occurrence of a characteristic fungous flora of the soil has been established. Waksman (1932) gives an up-to-date review of the subject, while later papers by various authors have extended the list of reported genera and species.

The constitution of the fungous flora varies considerably with the type of soil concerned, i.e. its structure, the abundance of organic matter, the reaction, the moisture content, etc., and with external conditions such as temperature. For example *Trichoderma* spp. are usually abundant in forest, heath, and other acid soils, while members of the Mucorales appear to preponderate in field and garden soils; Fusaria are typical of cultivated soils, and appear to be rare in virgin soils; Aspergilli characterize greenhouse soils and the soils of warm countries, while Mucorales and Penicillia are typical of the soils of colder climates. Certain genera and species have been isolated repeatedly from cultivated and virgin soils of all types, the commonest genera being *Mucor*, *Zygorhyncus*, *Rhizopus*, *Absidia*, *Penicillium*, *Aspergillus*, *Trichoderma* and *Fusarium*. It is also known that fungi occur to a depth of several feet in the soil (*Zygorhyncus Vuilleminii* and *Trichoderma Koningi* have been found at a depth of six feet), though the surface layer of six to eight inches is the most thickly populated. Bisby, Timonin & James (1935) investigating the fungi of different soil profiles in Manitoba, found that "high temperature fungi" (i.e. those which developed in plates incubated at 37° C.) notably Aspergilli and Trichodermae, predominated in surface soils, while "low temperature fungi" (developing in plates incubated at 6° C.), e.g. *Cylindrocarpon*, members of the Mucorales, and certain Penicillia, showed a great increase in numbers, relative to the total number of fungi present, with greater depth.

Quantitative studies have shown that the greatest numbers of fungi, present as actual mycelium in the soil, occur in acid soils rich in organic matter. Jensen (1931), however, examining a large

number of Danish soils of different types, found no close correlation between fungus numbers and soil type, except that heavy clay soils are poor in fungi. Nor did he find any close correlation between fungus numbers and soil reaction, though the ratio Number of Fungi : Number of Bacteria and Actinomycetes showed a very close relation to the reaction.

He found that fertilizers increased the numbers of fungi in the soil, also the addition of cellulose to the soil stimulated the development of fungi (except Mucorales) in both acid and alkaline soils, while the addition of glucose, casein, or alfalfa seed meal caused an increase of fungi in acid soil, but had less effect in alkaline soil. The number of fungi in the soil, therefore, would appear to depend primarily upon the amount of available food material, but also upon other factors.

The most extensive accounts of fungi isolated from the soil in Great Britain are those of Dale (1912, 1914) and of Bayliss Elliott (1930). Dale isolated and described fungi from sandy, chalky and peat soils, while Bayliss Elliott described the fungi of a salt marsh. The latter has also described, in 1933, some fungi isolated from heath soil.

So far as I am aware, very few studies of the fungi of pinewood soils have been made, though in various accounts of particular groups, especially of the Mucorales, species isolated from pinewood soil have been described. Hagem (1908) has described the Mucorales of a Norwegian pine forest; Rostrup (see Müller *et al.* 1910) isolated species of *Penicillium*, *Trichoderma*, *Mucor*, *Monilia*, *Oidium*, *Dematium*, *Hormodendron*, *Fusicola*, *Fusicladium*, *Citromyces*, *Pachybasium*, *Verticillium* and *Stysanus*, and four sterile mycelia, from heath soils planted with pine trees.

Species of *Trichoderma* and of *Zygorhynchus*, and *Mucor Rammanianus* appear to be particularly characteristic of acid forest soils, especially pinewood soils.

Methods

In the present work, samples of soil were collected in early autumn from a small wood, comprised mainly of *Pinus sylvestris*, a few miles from Nottingham. The surface layer of pine-needles and débris was first scraped away, and a small pit about a foot deep dug with a sterile trowel. Samples were taken from the side of the pit, at four inches and ten inches depth, sterile spatulas being used to transfer the samples to sterile containers, which were then sealed and transferred to the laboratory. At the same time, the reaction of the soil solution was tested, and was found to be *p*H 4·0.

The following media were used for isolation:

(1) Soil extract agar, prepared by boiling 1 kg. soil with 2 litres of water for 1½ hours, filtering, and bringing the reaction of the filtrate to *p*H 4·0, by the addition of normal H_2SO_4, before adding 2 % agar-agar.

(2) Waksman's glucose-peptone agar, consisting of glucose 10 g., peptone 5 g., $MgSO_4.7H_2O$ 0·5 g., water 1 litre. Enough normal H_2SO_4 is added to bring the reaction approximately to *p*H 3·8, and 2 % agar-agar is finally added before sterilization. The final reaction, after sterilization, is *p*H 4·0.

The media used for study and identification included Czapek's agar, 2 % malt-extract agar, potato-mush agar, cornmeal agar, bread, etc.

Two methods of isolation were used. In one, fragments of soil were placed directly upon the medium, and isolations were made after twenty-four hours of incubation at 22° C. This is the "direct method" advocated by Waksman for the isolation of fungi occurring as mycelium in the soil. In the second, samples weighing approximately 10 g. were shaken up with 100 c.c. sterile water, and plates inoculated with drops of the suspension. These plates were incubated at 22° C. for ten days, isolations being made as new colonies appeared, thus allowing fungi which may have been present only as spores in the soil to develop.

Account of fungi isolated

All the fungi enumerated below appeared repeatedly in different plates, and may be assumed to be characteristic of the soil under examination. A number of species which appeared only once or twice have not been included. In all, twenty-one species, belonging to eleven genera, were isolated and identified, also a sterile mycelium.

There seemed to be no appreciable difference in numbers of fungi between the two samples taken at different depths, plates inoculated with sample B (ten inches depth) by the indirect method showing about the same number as those inoculated with sample A. (A careful quantitative study was not made.) The same species appeared in plates made from both samples.

The only fungi isolated by the direct method were *Trichoderma* spp., *Botrytis cinerea*, and members of the Mucorales, the first-named being markedly predominant. Penicillia and an *Aspergillus*, which appeared in plates inoculated by the indirect method, appeared also in the directly-inoculated plates after several days' incubation. The delay in their appearance may well have been due to their slower growth being masked by the rapidly-growing species of *Mucor* and *Trichoderma* during the first twenty-four hours of incubation, rather than to the fact that they were present only as spores and not as mycelium in the soil. It is of interest to note that Jensen states that "the direct isolation method yielded mainly Trichodermae from forest, moor and heath soils, and mainly Mucoraceae from field, garden and salt marsh soils".

The following lists give the species found in the two samples by the different methods of inoculation.

Direct method of isolation

Sample A	Sample B
Botrytis cinerea Pers.	*Botrytis cinerea* Pers.
Mortierella hygrophila Linneman	*Mortierella hygrophila* Linneman
Mucor hiemalis Wehm.	*Mortierella gemmifera* nov. sp.
? *Mucor sylvaticus* Hagem	*Mucor hiemalis* Wehm.
Rhizopus nigricans Ehrenb.	? *Mucor sylvaticus* Hagem
Trichoderma Koningi Oud.	*Rhizopus nigricans* Ehrenb.
Trichoderma lignorum (Tode) Harz	*Trichoderma Koningi* Oud.
Zygorhyncus Moëlleri Vuill.	*Trichoderma lignorum* (Tode) Harz
	Zygorhyncus Moëlleri Vuill.

A sterile mycelium appeared in plates inoculated from both samples, but only after two or three days' incubation.

Indirect method of isolation (both samples)

In addition to the species listed above, the following were found:

Absidia spinosa Lendn.
Acrostalagmus cinnabarinus Corda
Alternaria tenuis Nees
Aspergillus Sydowi Bain. & Sartory (sample A only)
Mucor Rammanianus Moëller
Penicillium cyclopeum Westling (sample B only)
Penicillium spp. (Isolates 12, 13, 16, 17, 18)
Trichoderma album Preuss

Description of species

I. Fungi Imperfecti. *Acrostalagmus cinnabarinus* and *Alternaria tenuis* appeared in about a dozen plates inoculated from each sample by the indirect method, but neither species grew within twenty-four hours in plates inoculated by the direct method. Both have previously been reported from soil. The *Botrytis cinerea* strain appeared in about half the "direct method" plates, and in nearly every plate inoculated by the indirect method, and seems to be characteristic of this soil.

The green *Trichoderma* spp., however, were by far the most abundant, occurring in every plate and overgrowing the cultures so rapidly that it became difficult to isolate the other fungi present. A number of strains were isolated, but all of them fell distinctly into one or other of the two species *T. lignorum* and *T. Koningi*, differing only very slightly in colour and spore size. All the strains referable to *T. lignorum*, when grown on Czapek's agar or glucose-peptone agar, show a strong tendency to submerged growth, with a rather sparse, cobwebby, white aerial mycelium. On malt-extract agar the aerial mycelium is more strongly developed. Small tufts of conidiophores appear after about three days' growth, and become green as the conidia develop. These tufts may appear first at the centre of the

colony, or may not be formed until the mycelium reaches the edge of the dish, when a peripheral zone of tufts appears. In some strains the tufts are more or less uniformly scattered over the surface of the colony, while in others, especially on glucose-peptone agar, there is a distinct tendency to zonation. The bright green colour of the colony darkens with age. The dichotomously branching (occasionally trichotomous) conidiophores bear heads of about fifteen globose, bright green conidia, average diameter 2·8 μ. (One strain has slightly larger conidia, diameter 3·0–3·5 μ.) On pieces of sterile pinewood the fungus spreads rapidly, conidia appearing in four to five days, and after fourteen days the wood is covered with dark green, powdery growth.

The mycelium of the strains of *T. Koningi* resembles that of *T. lignorum* at first. After seven to eight days' growth dense tufts of conidiophores appear. These tufts are large and cushion-like, often 2–3 mm. diameter, and at first are separated by areas of more or less sterile mycelium. Later, as they become more numerous and increase in size, they become aggregated together and the culture becomes more uniform in appearance. They are bright green, and do not darken much with age. The conidial heads resemble those of *T. lignorum*, but the conidia are ellipsoid, average size 2·5 × 3·5 μ, and are much less deeply coloured when seen under the microscope.

On wood the growth is slower than that of *T. lignorum*, a few tufts of conidiophores appearing in about ten days.

A white *Trichoderma* was isolated about twelve times from samples A and B, by the indirect method. The mycelium resembles the green *Trichoderma* spp. in mode of growth, but is more delicate. After about seven days, white, sparsely distributed, conidial tufts, appear. These tufts consist of branching conidiophores, resembling those of the other species of *Trichoderma*, interspersed with single, spirally-twisted, septate hairs which project beyond the surface of the tuft. The conidia are colourless, globose and small, average diameter 2·0 μ (rarely elliptical 2 × 3 μ). The size and form of the conidia, and the characteristic hairs, suggest that this fungus is the *T. album* described by Preuss (1851). Dale (1912) isolated a white *Trichoderma* which she described under the name of *T. album* Preuss, but in her strain the spores were usually triangular, and the characteristic hairs described by Preuss were absent. Jensen (1931) reports, but does not describe, a *Trichoderma album* from a Danish soil, and other investigators have also reported the occurrence of white forms in various soils.*

II. Aspergilli and Penicillia. The only *Aspergillus* found in any of the plates was *A. Sydowi*, which appeared four or five times in plates from sample A only. It can hardly be regarded as characteristic of

* *Trichoderma*, when kept in culture for several months appears to have a tendency to lose its power of sporulation.

this soil. A strain of *Penicillium cyclopeum* Westling was found in sample B only, and was not frequent. It showed very marked coremium formation on malt extract agar and on bread.

Five other strains of *Penicillium* were isolated repeatedly from both soil samples by the indirect method (isolates 12, 13, 16, 17 and 18).

Penicillium (no. 13) is a member of the group Monoverticillata stricta-floccosa, with smooth, globose conidia 2·0–2·5μ in diameter. This strain closely resembles *P. restrictum* Gillman & Abbott, but differs in having smooth conidia.

Penicillium (no. 16) is a member of the group Biverticillata-symmetrica, and appears to belong to the *P. luteum* series. The conidiophores have an average diameter of 2·4μ, bearing metulae 8–9μ long and sterigmata 6–8μ long. The conidia are smooth, oval, 1·8–2·5μ in diameter.

The remaining three Penicillia (nos. 12, 17, 18) are members of the *P. Pfefferianum* series, closely allied to *P. spinulosum* and differing from each other chiefly in colour. No. 12 has divergent chains of globose, faintly spinulose conidia of average diameter 3·0μ. In no. 17 the chains of conidia tend to adhere in columns, while the conidia themselves resemble in size and form those of no. 12. No. 18 has divergent chains of spinulose conidia, globose or rarely elliptical, from 2μ diameter to 3·6 × 4·3μ.

Table I

Isolate	Conidial areas	Reverse
Penicillium no. 12	Tea-green XLVII 25'''' *f*, later deep greyish olive XLVI 21'''' *i*	Light olive-grey LI 23'''' *d*, later cinnamon drab XLVI 13''''
Penicillium no. 13	Glaucous XLVIII 37'''' *f* to dawn grey LII 35''''' *d*	Creamy
Penicillium no. 16	Asphodel-green XLI 29''' to pois-green XLI 29''' *i*	Primrose-yellow XXX 23'' *d*
Penicillium no. 17	Russian green XLII 37''' *i*, later slate-olive XLVII 29'''' *i*	Light pinkish cinnamon XXIX 15'' *d*, later mikado brown XXIX 13'' *i* to chocolate XXVIII 7'' *m*
Penicillium no. 18	Dusky blue-green XXXIII 39'' *m*	Primuline yellow XVI 19'
Penicillium no. 19	Deep bluish grey-green XLII 41''' *i*	Pinkish buff XXIX 17'' *d*, later snuff brown XXIX 15''

III. Mucorales. Four members of the Mucorales isolated were readily identified as *Mucor Rammanianus* Moell., *Zygorhyncus Moelleri* Vuill., *Absidia spinosa* Lendn., and *Rhizopus nigricans* Ehrenb.

Only the (+) strain of the *Rhizopus* was found. The *Absidia* and *M. Rammanianus* occurred several times in plates inoculated by the indirect method from both samples, but were not obtained by the direct

method. Jensen also failed to obtain *M. Rammanianus* by the direct method, for it grows slowly and is quickly overrun by other Mucors and by the Trichodermae, but it appears to be a characteristic member of the flora of pinewood soil.

The remaining two species of *Mucor* (isolates nos. 3 and 6) do not correspond exactly with the descriptions of any known species, but agree sufficiently closely with *M. sylvaticus* Hagem and *M. hiemalis* Wehm. to be regarded as strains of these species.

Mucor no. 3 most nearly resembles *M. sylvaticus*, a species found by Hagem in pine forest soil in Norway, differing from it chiefly in the smaller size of the sporangia and the greater average size of the spores. It forms on bread a white turf 1·5–2 cm. in height, turning greyish with age. The sporangiophores, of average diameter 6·5μ, show sparse cymose branching. (Lendner describes the branching of *M. sylvaticus* as racemose, Hagem as cymose.) The sporangia are 25–60μ, mostly 30μ diameter (*M. sylvaticus* Hagem has sporangia 45–70μ in diameter; Lendner states that the average diameter is 44μ, rather larger than the sporangia of the strain here described), membrane diffluent leaving a collarette, columella oval to spherical 7 × 10μ to 25 × 30μ.

Spores sometimes round, more often oval or elliptical, average size 5 × 6·6μ (Hagem describes the spores of *M. sylvaticus* as shortly cylindrical with rounded ends, 2·5–3·5 × 3·5–5μ, Lendner as oval or subcylindrical, very unequal in size, 2 × 4μ to 3 × 5μ, Zycha (1935) as oval or cylindrical, 2·5–3·5 × 4–5μ, sometimes as large as 4·5 × 7μ.) Chlamydospores are produced in the submerged mycelium, and are spherical, smooth-walled, 6·5–23μ diameter. Numerous azygospores with encrusted membranes, 30–70μ in diameter, are produced, frequently in pairs.

Mucor no. 6 appears to be a strain of *M. hiemalis* Wehm. It forms on bread a yellowish white turf about 1·5 cm. high. The sporangiophores are most frequently simple, but occasionally show racemose branching. Sporangia 18–60μ diameter, mostly about 45μ (rather smaller than those of typical *M. hiemalis*). Membrane diffluent, leaving a collarette. Columella oval, average size 18 × 21μ. Spores mostly elliptical, and very variable in size, from 3 × 4·5μ to 6 × 10·5μ. Chlamydospores produced occasionally, spherical or oval, 16–27μ in diameter. When plated out with (+) and (−) strains of *M. hiemalis* Wehm., this strain reacts with the (−) strain producing normal zygospores.

Of the two *Mortierella* spp. isolated, one agrees very closely with the description of *M. hygrophila* Linneman, differing chiefly in the smaller size of the spores. This species was found by Linneman (1936) in pinewood and other soils, and in cultures of aquatic fungi. According to her description, the submerged mycelium, in culture on solid

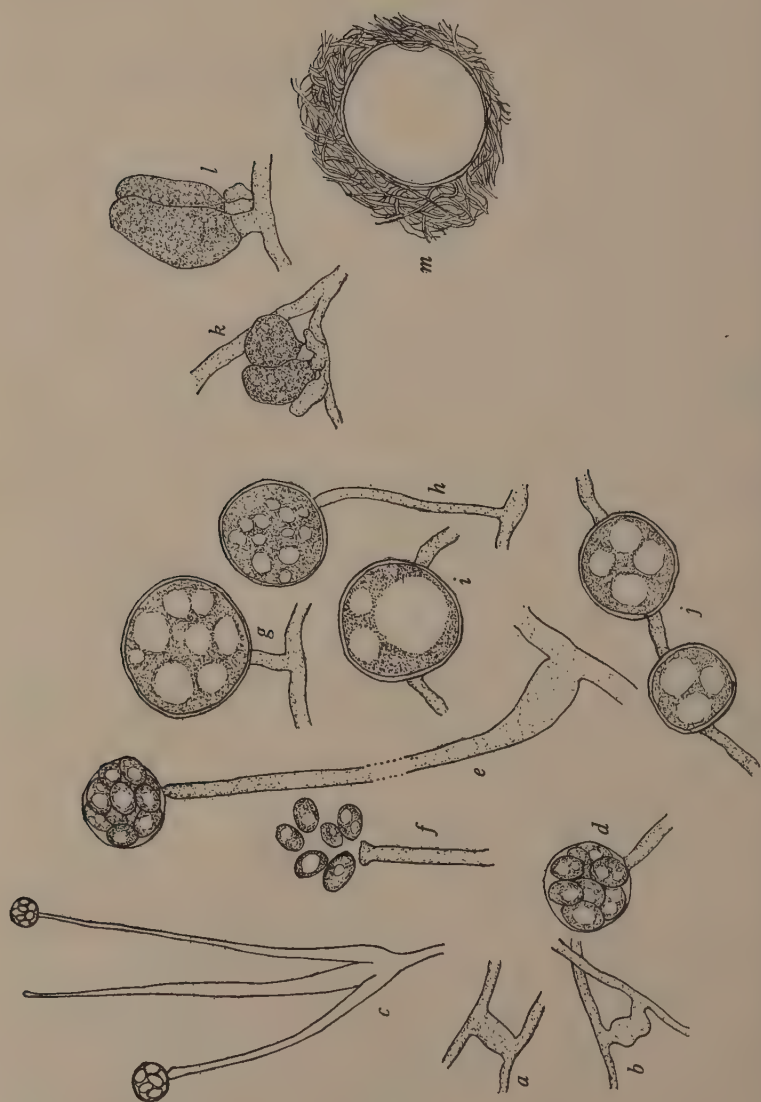

Fig. 1. *Mortierella gemmifera*. *a*, *b*, vegetative anastomoses; *c*, *d*, *e*, sporangia; *f*, dehisced sporangium; *g*, *h*, terminal gemmae; *i*, *j*, intercalary gemmae; *k*, *l*, early stages in zygospore formation; *m*, mature zygospore with part of hyphal sheath. *a*, *b* × 250; *c*-*l* × 500; *m* × 125.

media, forms broad, distinct zones or patches. The pure white aerial mycelium, which reaches a height of 1·5 cm., is richly branched and forms flocculent columns or a dense homogeneous mass.

The sporangiophores arise from stolon-like hyphae, and branch cymosely, the branches diverging at an angle of 45°. There may be as many as twenty branches, and cross-walls may be formed. Branching is especially profuse in water-culture. The sporangiophores may be up to 1 mm. long, usually 200–400 μ, but are sometimes small, thin and fragile. Columella only slightly arched, membrane diffluent leaving a collarette. The strain isolated by me agrees closely with the above description, but while the spores of the typical *M. hygrophila* are described as "irregular, round or oval, with a central oil drop, 8–25 μ diameter, mostly 16 μ", those of the strain in question are mostly oval, and measure 6–8 μ to 12 × 14 μ, rarely attaining a diameter of 16 μ. The number of spores in the sporangium varies greatly. Elongated chlamydospores, variable in size and shape, are found in old cultures.

The second *Mortierella* does not correspond with any species hitherto described. On bread a dense, cottony white turf about 1·5 cm. high is formed, while on malt-extract agar and similar media there is a tendency to submerged growth with irregular tufts and patches of aerial mycelium. Sporangiophores usually simple but sometimes cymosely branched, 100–300 μ long, tapering from 10–25 μ diameter at the base to 5–8 μ at the apex. There is sometimes, but not always, a constriction below the sporangium resembling that in *M. strangulata* van Tiegh. Sporangia are not abundant. They are spherical, 20–30 μ in diameter, with a diffluent membrane. No basal collarette appears to be left. Spores elliptical, average size 10 × 12 μ. Zygospores rather sparsely produced on malt agar, more abundant on corn meal agar and Czapek's agar, colourless, smooth-walled, 100–150 μ diameter. A thick hyphal sheath gives a total diameter of 0·5 mm. or more. A very characteristic feature is the production of numerous spherical, smooth-walled gemmae, 35–50 μ in diameter, which are particularly abundant on malt agar. They are borne either on short, slender, erect branches of the mycelium (resembling, apart from their smooth walls, the stylospores of other species of *Mortierella*) or in intercalary positions on the submerged mycelium. The name *M. gemmifera* is suggested by this characteristic.

Diagnosis. "*Mortierella gemmifera* sp. nov. Mycelio denso, albido; hyphis sporangiferis interdum cymose ramosis, sed plerumque simplicibus, 100–300 μ altis, versus apicem sensim attenuatis ab 10–25 μ ad 5–8 μ diam.; sporangis pallidis, globosis, 20–30 μ diam.; cuticulo diffluente, collari basilari haud persistente; sporis ellipsoidiis 10 × 12 μ diam. Zygosporis in "malt agar" et "cornmeal agar" bene evolutis, sphaericis, hyalinis, levibus, 100–150 μ diam., cum vagina hyphali

0·5 mm. Gemmis in "malt agar" optime evolutis, sphaericis, levibus, 35–50μ diam., cum denso protoplasmate et guttulis olei.

IV. The sterile mycelium appeared after several days in plates inoculated directly with soil, and also in several plates inoculated by the indirect method. It consists of fine, branching septate hyphae, and is white at first, later turning yellow. On Czapek's agar the reverse of the colony is at first pale yellow, rapidly becoming deep rose-pink, while on malt agar the reverse changes from yellow to orange. This fungus may be the vegetative mycelium of a Basidiomycete, possibly mycorrhizal.

Summary

Twenty-one species, belonging to eleven genera, were isolated from samples of pinewood soil. *Trichoderma* spp. and *Botrytis cinerea* preponderated, followed by Penicillia and members of the Mucorales.

Most of the species have been found in various soils by other investigators, and may be regarded as characteristic of acid forest soils in temperate climates. There appeared to be little or no difference between samples taken at four-inch and at ten-inch depths, the same species being present in both samples.

A new species of *Mortierella* is described.

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A STUDY OF *UROMYCES SCIRPI* BURR.

By MARGARET FORT

(With Plate IV and 11 Text-figures)

Introduction

Uromyces Scirpi Burr. is a heteroecious eu-form. The two stages of its life history were first connected in 1890, when Plowright found that *Aecidium Glaucis* and *Uromyces lineolatus*, infecting *Glaux maritima* and *Scirpus maritimus* respectively, were really part of the same fungus. In 1904, Sydow described the aecidial stage as occurring on *Hippuris* and various Umbellifers, amongst which was *Oenanthe crocata*, as well as on *Glaux maritima*. Grove (1913) described the aecidial stage appearing on *G. maritima*, but quoted Sydow as to the variety of hosts it might affect. In 1934, Grove and Chesters described the occurrence of the aecidial stage on *G. maritima* at Gorleston in Norfolk, though not on supposedly susceptible Umbellifers and *Hippuris vulgaris* which grew nearby, and also the appearance, at Saltash, in Cornwall, of aecidia on *Oenanthe crocata*, but none on *Glaux maritima* which grew in the neighbourhood.

In 1938, aecidia, uredospores and teleutospores, the former on *Oenanthe crocata* and the latter on *Scirpus maritimus* were found at the estuary of the River Eden in Fife. These agreed with the description given in Grove (1913) under *Uromyces Scirpi* Burr. This was the first record of the rust from Scotland (Macdonald, 1939). No infection of the neighbouring *Glaux* was seen. Work on the rust was therefore undertaken to determine the host relationships and to study certain aspects of the life history of the fungus.

Methods

Pieces of *Oenanthe crocata* and *Scirpus maritimus* material were fixed with Ble's fixative, or alcohol-formalin-acetic no. 2 (Rawlins, 1933). Some of the material was imbedded in paraffin, and microtomed at 15μ thick, and some was hand-sectioned. The stains used were Haidenhain's iron-alum-haematoxylin, counterstained with congo red in clove oil. As, however, the congo red did not give good results, iron-alum-haematoxylin was used alone, and found to be very satisfactory. Sections were also stained with alcoholic safranin, and aqueous safranin counterstained with light green in clove oil. Cotton blue in lactic acid was used for mounting some hand-sections as it shows up hyphae very clearly.

Inoculation experiments

Inoculation experiments were begun as soon as teleutospores from *Scirpus*, which had been kept in a tin outside all winter, had begun to germinate.

The time of germination was determined by mounting scrapings from teleutosori in drops of sterile water, on slides placed in Petri dishes, lined with damp filter-paper. This was done in October, January, February, the dishes usually being kept in the laboratory; though on one occasion two were placed outside. It was not till the thirteenth of February that general germination commenced, though one germinating teleutospore was seen in November and several on the ninth of January. Germination in all dishes took place at approximately the same time, whether set up in October, January, or February, whether placed outside or inside. Though there had just been a spell of hard frost, followed by several days mild weather, this would seem to have little bearing on the phenomenon, as some of the material had been artificially frozen in October, by surrounding it with pieces of ice, with no consequent effect on the time of germination. Also some of the teleutospores, i.e. those which were set up in October, had not been subjected to frost, as they were kept in the laboratory.

Germinating uredospores were also seen on the thirteenth of February.

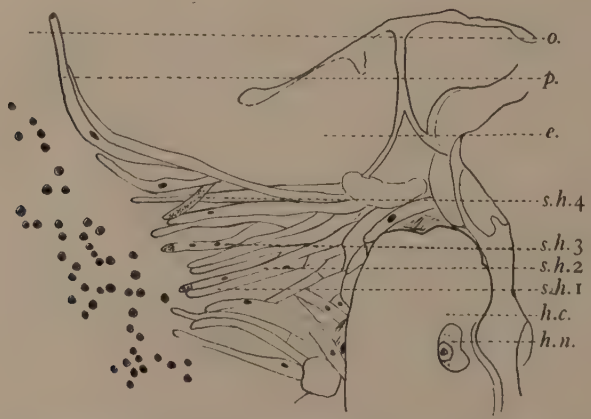
Three methods of inoculation were tried. The first consisted of placing a suspension of teleutospores in water on the leaves of a potted *Oenanthe crocata* plant, which had been well-watered. The second consisted of placing pieces of well-soaked teleutospore-bearing material on the surface of the soil of a similar plant. After both these methods the plant was kept under a bell-jar for a day to facilitate the germination of the basidiospores and entrance of mycelium. As these were both unsuccessful they were abandoned in favour of a third, which was that used by Lamb (1935). This method was used principally with teleutospores, and so was used to inoculate *Oenanthe crocata* and *Glaux maritima* plants. The inoculation of the *Glaux* plants was unsuccessful, but that of the *Oenanthe* plants highly successful.

Table I shows the number of experiments done, and the time taken after inoculation for each infection to appear.

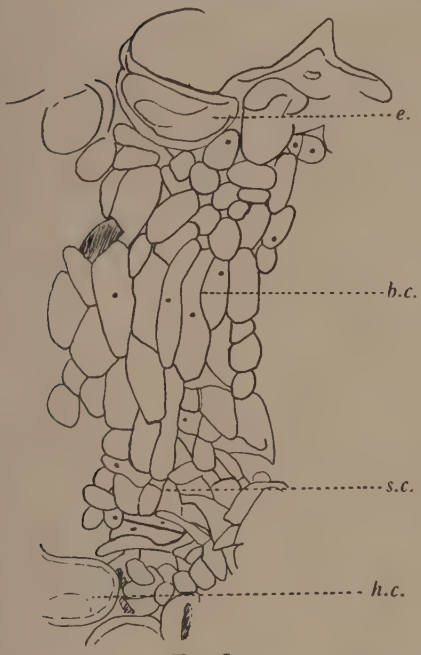
Table I. *Infection of* Oenanthe crocata

No.	Date of inoculation	Date of infection	Time taken
1	23 February	13 March	18 days
2	10 April	24 April	14 days
3	12 April	24 April	12 days
4	14 April	24 April	10 days
5	20 May	26 May	6 days

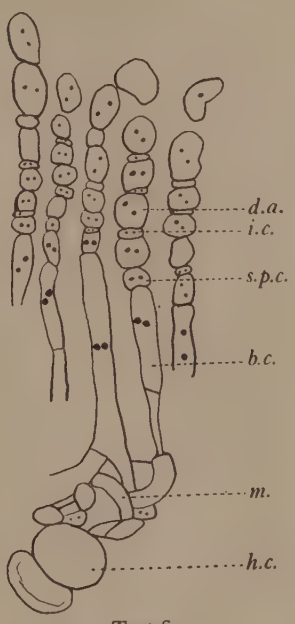
Text-fig. 1. Transverse section of *Oenanthe crocata* petiole with aecidium opening inwards instead of outwards, aecidiospore (*a.*), aecidial chains (*a.c.*), cortex (*c.*), hyphal weft (*h.w.*), pith (*p.*), pseudoperidium (*p.s.*). ×960.



Text-fig. 2. Transverse section part of spermogonium. Epidermal cell (*e.*), host cell (*h.c.*), host nucleus (*h.n.*), ostiole (*o.*), paraphysis (*p.*), spermatial hypha composed of long and smaller cell (*s.h.* 1), spermatial hypha with spore forming at end (*s.h.* 2), spermatial hypha with division of nucleus (*s.h.* 3), spermatial hypha full of cytoplasm (*s.h.* 4). ×790.



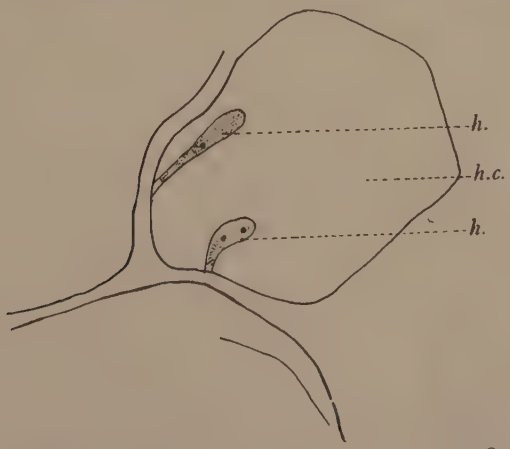
Text-fig 3



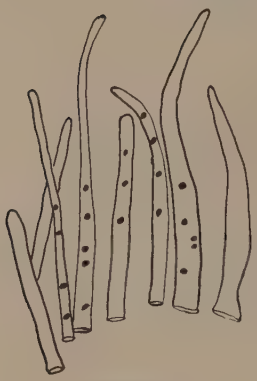
Text-fig 4

Text-fig. 3. Transverse section part of immature aecidium, buffer cells (*b.c.*), epidermis (*e.*), host cell (*h.c.*), sporogenous layer (*s.c.*). ×480.

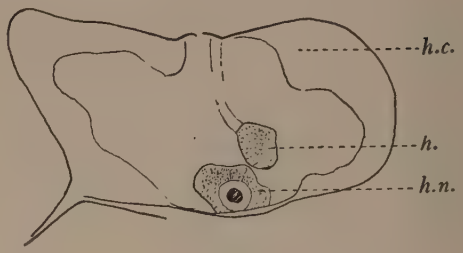
Text-fig. 4. Aecidial chains, basal or fertile cell (*b.c.*), developing aecidiospore (*d.a.*), intercalary cell (*i.c.*), mycelium (*m.*), spore mother cell (*s.p.c.*), host cell (*h.c.*). ×480.



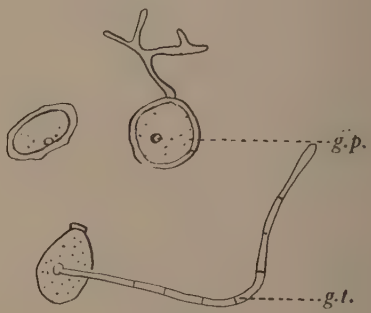
Text-fig. 5. Host cell (*h.c.*) with haustorium (*h.*). ×960.



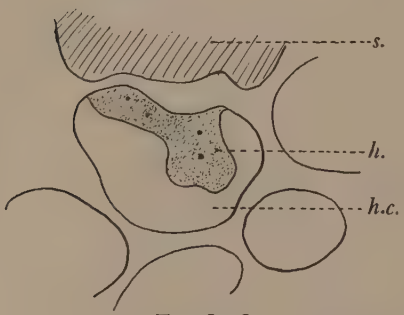
Text-fig. 8



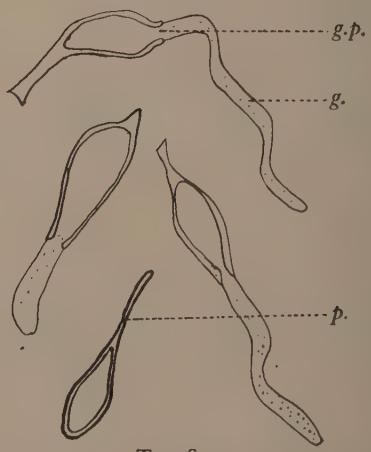
Text-fig. 7



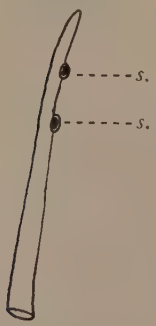
Text-fig. 10



Text-fig. 6



Text-fig. 11



Text-fig. 9

Text-fig. 6. Host cell (*h.c.*) from just under spermogonium (*s.*) showing multinucleate haustorium (*h.*). × 960.
Text-fig. 7. Host cell (*h.c.*) with haustorium (*h.*) near the nucleus (*h.n.*). × 960.
Text-fig. 8. Group of multinucleate paraphyses from ostiole of a spermogonium. × 960.
Text-fig. 9. Paraphysis from the same spermogonium as those in fig. 8 with spermatia (*s.*) attached. × 960.
Text-fig. 10. Uredospores, germ pore (*g.p.*), germ tube (*g.t.*). × 380.
Text-fig. 11. Teleutospores, germ pore (*g.p.*), germ tube (*g.*), pedicel (*p*). × 380.

Infection is marked by a yellowing of the plant tissues, and followed by the appearance of spermogonia. These appeared on the dates given above under "Date of infection" as minute orange dots, and opened the following day, when drops of exudate were distinguished. When viewed from the side the paraphyses can be seen projecting beyond the epidermis. A flower-like odour has been mentioned as emanating from spermogonia but none could be detected here. The spermogonia are produced in patches, usually about seven in a group.

About the twenty-second day the first signs of aecidia are seen, and these open about eight days later. A noticeable feature of their position is that they tend to grow in the furrow of the petiole or on the ridges, and in the leaf, on the veins.

Lamb's method was also used for inoculating *Scirpus* seedlings by means of uredospores, but as these were rather scarce the extra precaution of obtaining them from scrapings from teleutosori and transferring them in a drop of water to the *Scirpus* plant was taken. No infection was obtained from this experiment. Inoculation of *Scirpus* by aecidiospores from *Oenanthe crocata* was done by leaving a *Scirpus* plant in a cool frame where the infected *Oenanthe* plants were kept. Uredosori were first seen on the *Scirpus* plant on 1 June, but no time taken for infection to develop after inoculation can be given as the time of inoculation is uncertain.

General description of rust

The spermogonia and aecidia of the rust occur on the petioles and leaves of *Oenanthe crocata*, as minute dots. The spermogonia are orange, and visible chiefly because of the drop of sticky secretion which they exude. They appear in groups. The aecidia too, are orange, and are cup-shaped, occurring in groups. The tissues round the aecidia tend to be swollen and yellowed. In some places, particularly on a dying leaf, green lines are present round the infected areas. It has been suggested (Rice, 1935) that such lines are due to the fungus actually having a beneficial effect on the host cells, and stimulating the protoplast and hence the chloroplasts.

Spermogonia and aecidia tend to grow on the collenchymatous ridges of the petiole. This is especially noticeable in the former. When not on the ridges they are situated in the furrow on the upper side. The presence in the furrow of spermogonia may be due to the effect of gravity on drops of water present on the plant when inoculated. This is confirmed by the appearance of large infections, where two leaflets meet the petiole in such a way as to present a hollow in which water would be expected to collect.

In transverse section, of the petiole or leaf, the spermogonia appear as flask-shaped structures opening to the outside. In the leaf the

spermogonia, though more frequent on the upper side, are not confined to it, but occur on the lower as well. They have a tendency in the leaf to grow on the veins.

In a transverse section of the petiole the aecidia open to the outside (Pl. IV, fig. 1), as a rule, but occasionally they are found inside the tissues, particularly in the aerenchymatous pith, where they occupy an air space (Pl. IV, fig. 2). One was found growing the normal depth below the epidermis but opening inwards instead of outwards (Text-fig. 1). This would appear to confirm Colley's opinion (1917), that aecidia produced in the pith or cortex are abnormalities with no special morphological significance. A possibility, suggested by the fact that aecidia in the pith open into the air spaces, is that the aecidium originated near one of the occasional cortical air spaces and, taking the path of least resistance, opened into it.

Aecidiospore measurements were 20–28 × 16–26μ. Grove (1913) gives the following figures: 16–24 × 14–20μ.

The uredo- and teleutosori appear on both sides of the leaves, on the leaf sheaths, and the inflorescence stalks of *Scirpus maritimus* as brown streaks. The uredosori are lighter in colour than the teleutosori.

Uredospores are globose to ovate and yellowish brown. The outer coat bears minute protuberances. There are three equatorial germ pores. Spore measurements obtained were 22–30 × 18–21μ (22–25 × 16–25μ Grove). On germinating they produce a thin-walled germ tube from one of the germ pores. The germ tube soon becomes septate (Text-fig. 10).

Teleutospores are borne in dark brown sori. The spores are pale brown, smooth and club-shaped. They taper above to the apical germ pore. The wall round this is thickened. The pedicels are brownish and persistent. The measurements of these spores are 27–48 × 13–21μ (26–45 × 15–21μ Grove). On germination the teleutospore produces a hyaline tube from the germ pore at the upper end of the spore (Text-fig. 11). This tube bears sterigmata and basidiospores.

Cytology of the rust

The internal appearance of petioles or leaves of *Oenanthe crocata* is more or less normal in a fairly heavy infection, except for the fungal threads which traverse and often fill the intercellular spaces (Pl. IV, fig. 2). This is especially so in the pith, where air spaces abound, but in a very heavy infection the spaces may be so filled that the individual host cells are isolated in the fungal wefts. These host cells appear quite healthy. Invasion of the host cells takes place by haustoria. As a rule these are simple, allantoid structures full of protoplasm (Text-fig. 5), though a compound one was found at the base of a spermogonium (Text-fig. 6). No effect on the host nucleus

is visible. No sheath was seen round the haustoria (Text-figs. 5–7). The hyphae tend to be irregular in outline and branching. Particularly in the air spaces of the pith they are covered with minute, shining globules. As it has been found that accumulation of starch is a characteristic of infection by some rusts (Gwynne-Vaughan & Barnes, 1937), these were tested for starch but the result was negative.

In preparations where aecidial infection was heavy, large cells were frequently found, elongated at right angles to the epidermis, and giving the appearance of palisade cells. These occurred in the cortex and seemed to take the place of the assimilating cells of a normal petiole. They contained no chloroplasts and occurred where there were several aecidia in close proximity to one another (Pl. IV, fig. 1 and Text-fig. 3). They were not seen where spermogonia were produced. It is probable that these cells, together with large quantities of mycelium, are the cause of the hypertrophy of the host and being free of chlorophyll, account for the yellow appearance of infected areas.

The spermogonium is composed of spermatial hyphae which grow in from the closely intertwined hyphal network which surrounds the spermogonium. The hyphae are thus arranged to form a globose structure, which has a cavity in the centre. Each spermatial hypha consists of a long cell, containing one nucleus (Text-fig. 2). There may be in addition, a small cell at the base of a long one. These long cells, besides containing one nucleus, have varying amounts of cytoplasm, according as the hypha is young or old. In the formation of a spermatium the cytoplasm moves up to the top of the hypha, and the nucleus divides into two, one part moving up to the tip of the spermatial hypha. There a cell wall is formed and the spore is cut off. This spore, the spermatium, is an oval thin-walled body with a large nucleus and very little cytoplasm. The spermatia fill the cavity in the spermogonium, and are carried out of it in a sticky secretion. The origin of this exudate is obscure, but it is here suggested that certain cells which are full of cytoplasm, and interspersed with the spermatial hyphae may form it. The opening of the spermogonium to the outside is small, and is lined with paraphyses, which resemble the spermatial hyphae very closely, but which are sterile. They turn outwards through the ostiole, and project through it in a brush-like tuft, giving the spermogonium its flask-shaped appearance. In some preparations spermogonia were found in which the paraphyses blocked the ostiole, and the exudate was dried on the surface of the leaf. Spermogonia of this type have been considered as dead (Allen, 1933). Spermatia were seen adhering to paraphyses in some spermogonia (Text-fig. 9), but there was no indication whether they were products of that particular spermogonium or of another. Paraphyses were also found with several nuclei, sometimes as many as five being present (Text-fig. 8).

Paraphyses containing many nuclei have been suggested as a possible means of entrance of the spermatia (Allen, 1933).

Apart from the paraphyses, this stage of the fungus was uninucleate.

In some sections, immature aecidia were seen. These were composed of a hyphal weft, the cells of which contain cytoplasm, surmounted by large cells, which are more or less empty, and are called sterile or buffer cells (Text-fig. 3). The function of these cells is thought to be that of crushing the host cells of the cortex, thus making way for the aecidial chains which develop from the sporogenous layer. These aecidia are uninucleate but may have occasional binucleate cells in them. The aecidial primordia originate about five cell-layers below the epidermis.

Mature aecidia are cup-shaped structures. They consist of basipetal chains bearing aecidiospores (Text-fig. 4). Each chain consists of a large elongated cell, the basal or fertile cell, which arises at right angles to the tangential cells of the hyphal weft, and which bears a globular spore mother cell above it. Both the basal cell, and the spore mother cell, are binucleate. Each spore mother cell abstricts aecidiospores, each of which cuts off from its base a small intercalary cell. The intercalary cells, as the aecidiospores attain maturity, degenerate and finally disintegrate. Suggestions of two-legged cells, found in other rusts, were seen here too, but were very occasional. The aecidial chains are enclosed in a pseudoperidium, composed of roundish cells tending to be polygonal, which seem empty, and resemble the aecidiospores in arrangement and size. No intercalary cells were seen associated with them.

The cells of the mycelium on *Scirpus maritimus* are binucleate.

Conclusion

Attempts to produce aecidia of *Uromyces Scirpi* on *Glaux maritima*, by inoculation with teleutospores, failed repeatedly and no natural infections were found though the *Scirpus* and *Glaux* hosts grow close together. On the other hand, aecidia were easily produced on *Oenanthe crocata* by artificial means and are found freely in nature in the same places when *Glaux* remains uninfected. It seems clear, therefore, that *Uromyces Scirpi* is a rust which shows specialization in the aecidial stage and that the form of the rust which occurs on *Oenanthe* will not infect *Glaux maritima*. The presence of germinating uredospores on *Scirpus maritimus*, in the early spring, indicates how it is possible for the aecidial stage to be cut out. Once this break in habit has occurred the chance of the introduction of a new aecidial host must be greatly increased.

Observations made on the rust on *Oenanthe crocata* showed that binucleate cells regularly make their first appearance at the base of the

developing aecidium. The spermogonia normally are uninucleate except for the paraphyses. These are frequently binucleate or multinucleate. Spermatia are often seen adhering to them and fusions apparently occur. Though it is impossible to prove the origin of such spermatia it is probable that some come from other spermogonia and that, after one comes in contact with a paraphysis, its single nucleus passes in. The products of the division of such a nucleus could reach, by migration, the aecidial primordium with its uninucleate cells and there initiate the binucleate phase as, for example, in the manner described for *Puccinia Phragmitis* by Lamb.

Summary

1. All stages of *Uromyces Scirpi* have been found near St Andrews. Uredo- and teleutospores on *Scirpus maritimus*; spermogonia and aecidia on *Oenanthe crocata*. No aecidia were present on *Glaux maritima*.

2. Inoculation experiments repeatedly brought about infection of *Oenanthe* but not of *Glaux*. *Scirpus maritimus* was artificially infected from *Oenanthe crocata*.

3. The mycelium on *Scirpus maritimus* is binucleate, that on *Oenanthe crocata* is uninucleate till after the production of spermatia. Multinucleate spermogonial paraphyses are often found with adhering spermatia. Binucleate cells appear regularly in the base of the developing aecidium and the aecidiospores are binucleate.

4. It is suggested that the aecidia found on *Oenanthe crocata* belong to a different specialized race of *Uromyces Scirpi* from those occurring on *Glaux maritima* elsewhere. Further, that the binucleate condition is due to the migration to the aecidial initials of the products of the nucleus of a spermatium which has fused with and entered one of the spermogonial paraphyses.

The writer wishes to acknowledge the supervision received and the facilities placed at her disposal in the Botany Department of the University, St Andrews.

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EXPLANATION OF PLATE IV

Fig. 1. Transverse section of *Oenanthe crocata* petiole showing three aecidia (*a*) in the furrow, and palisade-like cells (*e.c.*). ×67.
Fig. 2. As in fig. 1, showing internal aecidium (*a*), elongated cells (*e.c.*), hyphal network under the aecidium (*h*), hyphal wefts in air spaces in the pith (*h.w.*). ×67.

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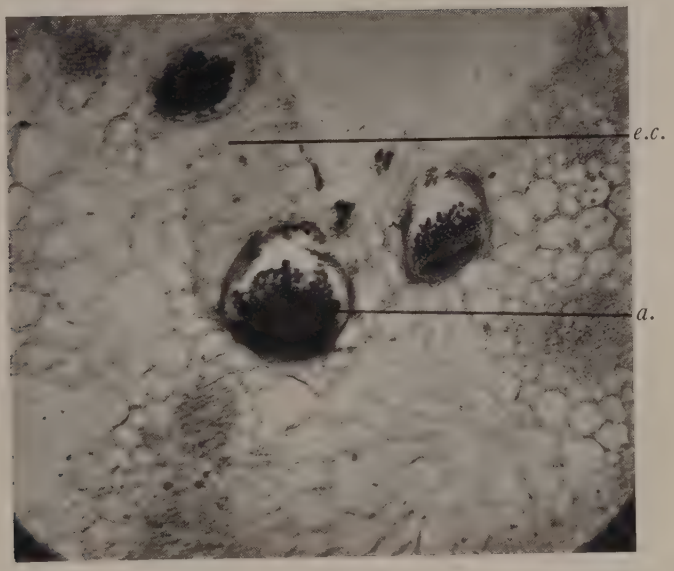

Fig. 1

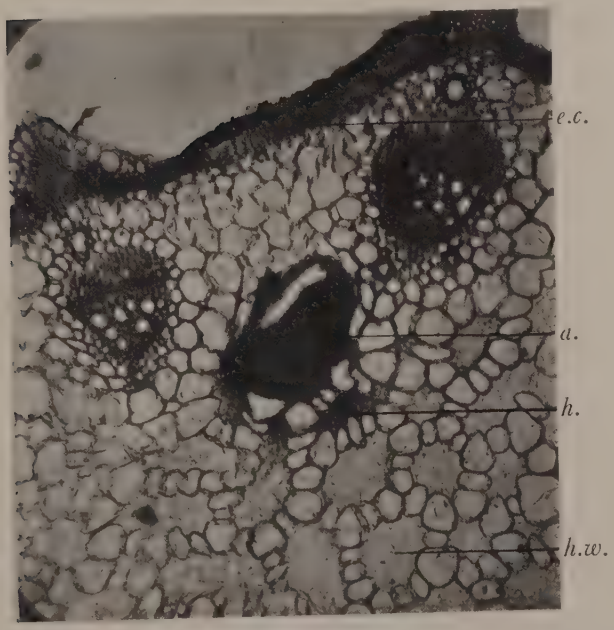

Fig. 2

EXAMINATION OF *AECIDIUM LEUCOSPERMUM* D.C. FROM SCOTLAND

By E. O. CALLEN, Ph.D.
Department of Mycology, University of Edinburgh

(With 1 Text-figure)

In the Royal Botanic Garden, Edinburgh, there is a patch of *Anemone nemorosa* infected with *Aecidium leucospermum*, which has been there for at least twelve years, but with no sign of other spore stages on the surrounding plants. This species is well known on account of its repeating aecidium, but in the course of four years' observations, the fungus has not been observed to spread to other plants of *Anemone* in the same bed.

Dowson (1912), working on *Aecidium leucospermum* from *Anemone nemorosa* collected near Hamburg, found that the mycelium was perennial in the rhizome, though otherwise quite normal, for the mycelial cells were uninucleate, and the peridial cells and aecidiospores were all binucleate. Kursanow (1917) on the other hand, worked on material from *Anemone ranunculoides* collected in the neighbourhood of Moscow, and found that there were two distinct forms, which grew on separate plants. In the uninucleate form, a relatively large number of aecidiospores (up to 5 %) were binucleate, but in most of these the binucleate condition was secondary, that is to say, an occasional spore in a uninucleate chain was binucleate. There were, however, a few chains in which all the spores were binucleate, and these arose from binucleate basal cells.

The nuclear condition of the Scottish material therefore seemed worth investigation, especially because re-infection of the *Anemone* is almost unknown.

On the Scottish material, spermogonia were produced at the beginning of March, and were fully mature towards the end of the month. They occurred on the upper surface of the leaf, and shrivelled up towards the end of April. The aecidia were first visible to the naked eye about the end of March, and reached maturity a month later. They were plentiful, but were at first to be found only on the lower surface of the leaf, though a few were later produced on the upper surface. Neither Dowson nor Kursanow mentioned the spermogonia, though they have been recorded by other investigators.

An examination of the aecidia showed that the spores were uninucleate, with an occasional chain of binucleate spores. Some aecidia had no binucleate chains in them, whilst others had three or even four binucleate chains, and as Kursanow observed, these were distinguishable from the uninucleate ones by their greater height in the earlier stages of development of the aecidium. The binucleate spores can usually be distinguished by their greater size.

On several occasions a binucleate spore was observed, which could not be traced to any binucleate chain, and which appeared to be the terminal spore of a uninucleate chain. One of these spores, which, owing to its size could be described as a mammoth spore, appeared to have originated from the fusion of the terminal cells of two uni-

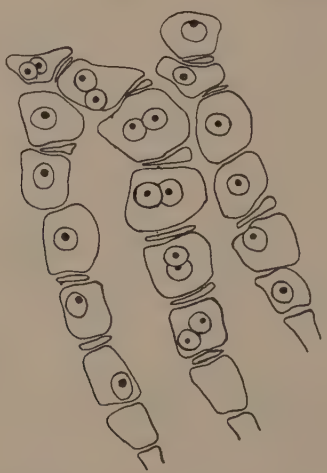

Fig. 1. *Aecidium leucospermum*, chains of aecidiospores. × 440.

nucleate chains. The other binucleate terminal spores apparently did not arise in this way. Kursanow figured a uninucleate chain with a single binucleate spore in the centre. This has also been observed in the Scottish material, though not nearly as frequently as Kursanow states. In the Russian material of *Aecidium leucospermum*, Kursanow stated that the predominant type of binucleate spore was of this latter type, that is, single spores in uninucleate chains. This was not so with the Scottish material however, where whole binucleate chains were the predominant type.

An examination of the peridial cells, showed that they were uninucleate as was to be expected. With regard to the *Anemone* leaves, Grove (1913) stated (p. 331): "The leaves become longer, narrower and of a paler green, and are borne on longer petioles. They are often

divided into more segments than the normal leaves." This was not so in the Edinburgh material. The leaves were smaller and of a paler green, but were certainly not divided into more segments, nor were the petioles longer. Each normal *Anemone* leaf is built up of three leaflets, with two of them usually very deeply cut, making it look like five leaflets. In infected specimens the three leaflets were still produced, but were not nearly so deeply cut, and there were fewer lobes on each segment. The petioles were shorter, or at most as long as those of the uninfected plants surrounding them, though other material of *Aecidium leucospermum* collected in Scotland showed the longer petioles.

Kursanow found that the uninucleate spores germinated readily in a damp chamber, but infection experiments on *Anemone ranunculoides* and *Sorbus Aucuparia* (the alternate host of *Aecidium leucospermum-Ochropsora Ariae* (Fuck.) Ramsb.) all proved negative. Using the Scottish material, infection experiments were carried out on young trees of *Pyrus Malus* (cultivated apple) and *Sorbus Aucuparia*, as well as on mature plants of *Anemone nemorosa* from several sources, but the results were entirely negative. Soppit (1893), however, demonstrated that re-infection of the *Anemone* can be obtained. He expressly stated that his attempts to infect mature plants of *Anemone nemorosa* had been unsuccessful, but on using seedling plants, he obtained aecidia on them in the following spring. The fact that young plants were used has apparently been overlooked by other investigators. It is hoped that further infection experiments may be carried out next spring.

I wish to thank Dr Malcolm Wilson, at whose suggestion this investigation was carried out.

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REVIEWS

Le Genre Mycena. Par ROBERT KÜHNER. Pp. 710. Paris: Paul Lechevalier. Frs. 300.

Dr R. Kühner, has produced a remarkable monograph, one which will be the standard work on the genus *Mycena* for many years to come; all that is missing is coloured plates of the species—we hope they will be forthcoming in a subsequent volume. The method followed is unlike that in his monograph of the genus *Galera*, where he was inclined to overload his descriptions with unessential detail. The diagnoses are, however, complete, and give a clear view of the species and varieties. They are accompanied by line drawings of the microscopic characters, and supplemented by drawings and descriptions supplied by eminent colleagues. He has not thought it necessary to give an outline of the spore of most of the species; an unfortunate omission, in our opinion. The classification is new. The primary division is into species with amyloid spores (*Eu–Mycena*) and non-amyloid spores (*Para–Mycena*), though he has had to place at least two species with non-amyloid spores in the first group, because they were too nearly related to other species to bear separation. *Mycena pseudopura* Cooke is maintained as a species, the spores not turning blue in iodine as contrasted with *M. pura* which has amyloid spores.

Further grouping follows partly the Friesian system with many modifications based on microscopic characters. Cystidia play a large part in the diagnoses. Our only criticism is that in a few species the author has adopted epithets that go counter to tradition. A few examples may be given of common species familiar to British mycologists:

M. ammoniaca Fr. becomes *M. metata* (Fr.?) sensu Schröter.
M. metata Fr. becomes *M. vitrea* (Fr.?) var. *tenella* (Fr.?) sensu Ricken.
M. vitilis Fr. becomes *M. filopes* Fr. (ex Bull.?) sensu Schröter.
M. filopes (Bull.) Fr. becomes *M. vitilis* (Fr.?) sensu Ricken.

Dr Kühner's explanation of such changes is that he has felt bound to adopt the name as applied to the first complete description giving microscopic details. This is a sound method, but should hardly be followed where there has been an obvious mistake in determination. We are not bound to accept Dr Kühner's nomenclature, but in using our more traditional names we shall have to make it clear in what sense we intend them.

In the preparation of this monograph the author has used in an impressive manner all the technical resources open to modern mycologists. Fortunately, this technique is not necessary for the determination of species. Two general keys are provided, and keys to each group which we have found very helpful.

Kühner has transferred a large number of *Omphalia* species to the genus *Mycena*. There were already several Mycenas with decurrent gills; for instance *M. rorida*, *M. cinerella*, *M. epipterygia* and *M. vulgaris*, and Fries included many Omphalias in his section "Mycenarii". On the whole, Kühner's view is probably sound, but will not appeal to everybody. He has with less justification and rather hesitatingly transferred a few species with amyloid spores from other genera, including them in a group "Spuriae", with the proviso that they may eventually go into independent genera. Many American species are described, thanks to the co-operation of Alex. H. Smith. Latin diagnoses of new species appear at the end of the volume.

In the preface a full account of the genus *Mycena* is given. The author himself has worked out the cytology of a large number of species, and gives a detailed and well illustrated account of the nuclear developments. Dr René Maire provides an introduction. The work is indispensable to all serious students of the Agarics.

A. A. PEARSON.

Les Champignons Toxiques. Par R. Dujarric de la Rivière et Roger Heim. Paris: L'Encyclopédie Médico-Chirurgicale. 1938. Frs. 45.

The authors of this work have brought together all the available information on the subject of the toxic qualities of fungi and the appropriate medical treatment. They are well qualified to undertake this task. Dr Heim is the Assistant Director of the Cryptogamic Department of the Natural History Museum in Paris, and Dr Dujarric de la Rivière, of the Pasteur Institute, has specialized in the treatment of fungus poisoning; he discovered, or rather perfected, the serum which seems likely to prove the most effective curative agent against poisoning by *Amanita phalloides* and its relatives, *A. verna* and *A. virosa*. The delayed symptoms and the complicated effects render medical treatment extremely difficult, and death has resulted in at least 50 % of the cases recorded. The serum constitutes the best treatment, but the chances of having it available when needed are remote. German physicians have experimented with glucose injections, with some good results. A successful treatment in 1936 by a French doctor suggests possibilities. Not being able to obtain the serum, he gave his patients, every half hour, a glass of cold water with a spoonful of sea salt added. The effect was immediate. The patients ceased vomiting, rallied, and were ultimately cured. Confirmation of the results of this simple treatment is needed.

Fortunately, the other forms of fungus poisoning are less serious. These forms are classified into ten categories, chiefly according to symptoms: whether affecting the cell tissues, nervous system, intestines, blood, muscular fibres, lungs, etc. Most species possessing some toxic quality come into one only of the categories; a few overlap into others. *Lepiota helveola* sensu lato is attached to the phalloidian category, but has not the same catastrophic effects. Deaths are reported from time to time as due to the consumption of fungi other than *Amanita phalloides*, but they are rare, and often due to subsidiary causes. Personal idiosyncrasy is doubtless an important factor. There is much contradictory evidence as to certain species which many people can eat with impunity and even relish, whilst others suffer serious digestive consequences; the mushrooms that turn yellow are best known in this respect, but other species recommended as edibles are in the same class such as *Clitocybe nebularis*, *C. geotropa*, *Tricholoma irinum*, etc. Among the species of *Russula* all the mild species are good, and the acrid ones either nasty or indigestible; though we remember meeting a Lett woman in Epping Forest, gathering *Russula emetica* for the pot and rejecting all others because her husband preferred it.

Some species with a sinister reputation have been rehabilitated in recent years, such as *Amanita mappa* and *Volvaria speciosa* (= *V. gloiocephala*). The first is not worth eating, but harmless, whilst the second is considered of culinary importance in some parts of the world. The suspect species of *Lactarius* such as *L. torminosus* are no longer looked upon as dangerous, and *Lactarius piperatus* is much appreciated by many mycophagists. Practically all species of *Boletus* are edible, even those that turn blue, with the exception of *Boletus satanas* which is indigestible. The wildly intoxicating effects of *Amanita muscaria* are well known, but statistics show that *Amanita pantherina*, which also affects the nervous system, has caused more deaths. Some of the white species of *Clitocybe*, especially *C. rivulosa* and *C. dealbata*, and many species of *Inocybe* seriously affect the nervous system. *Entoloma lividum* and *Tricholoma tigrinum* produce gastric troubles, and if you want a good purgative, *Clavaria formosa*, *Entoloma rhodopolium* and *E. nidorosum* will have the desired effect. *Coprinus atramentarius* does no harm to water drinkers, but may give a bad time to those who drink wine or any other alcoholic beverage, even some hours afterwards. Among the Discomycetes, *Gyromitra esculenta*, in spite of its name, has frequently been the occasion of serious trouble when consumed fresh without pouring away the water it is boiled in; it is, however, perfectly safe in the dried state, and large quantities are sold.

Most of this information was already familiar to mycologists, but it is useful to have it epitomized in this volume, which also has a complete list of the literature and eight coloured plates from the brush of M. Bessin. It is an invaluable addition to the library of the mycologist and especially to that of the physician.

A. A. Pearson.